HARD SUBSTRATES AS A LIMITING RESOURCE STRUCTURING INVADED COMMUNITIES WITHIN A CENTRAL CALIFORNIAN ESTUARY

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-ABSTRACT-

With increasing population pressure, estuaries face multiple anthropogenic disturbances. This dissertation explores the effects and interactions of human disturbances on species distribution and community composition within Elkhorn Slough, a central Californian estuary. I examine if direct anthropogenic habitat alteration through structural additions (bridges, harbors, pilings) enhances spatial distribution of non-native species and if structure-creating non-native species enhance abundances of other non-natives through habitat provision. Fouling species surveys and constrained linear ordinations show location within Elkhorn Slough and hard substrate variety and stability/size are important predictors of native and non-native species distributions. The location effect indicates unmeasured abiotic or biotic factors that vary throughout the system (pollution, predation pressure, recruitment) and influence species distributions. Several non-natives only occurred on anthropogenic hard substrates, suggesting that their persistence and distribution within Elkhorn Slough are facilitated by human structural additions. By following the development of assemblages on recruitment plates deployed at ten sites for 2.5 years, I show that recruitment limitation and fluctuating environmental parameters (salinity) vary among sites, and influence assemblage development. Biotic interactions, namely competition between bryozoan colonies, appear to occur only at locations where plate space is limited. The non-native reefs, formed by the tubeworm *Ficopomatus enigmaticus*, provide structure for abundant non-native amphipods and polychaetes. A reef removal experiment shows this non-native habitat influences benthic community structure by decreasing infaunal abundance, apparently through reduced water flow and anoxia in underlying sediments. Similarly high abundances of associated non-natives were not observed in the biogenic habitat created by the native oyster *Ostrea conchaphila*. In contrast, associated natives were common in both biogenic habitats but varied among sampling locations. The anthropogenic disturbance of substrate addition, both through added structures and species introductions, increases the spatial extent and abundance of associated non-native species in this soft-sediment estuary, suggesting that control of hard substrates may help control non-native species. The introduction of non-native ecosystem engineers results in abundant associated non-natives, representing a mechanism for invasional meltdown, namely the facilitation of associated non-natives through non-native biogenic habitat provision. This thesis demonstrates how anthropogenic disturbances can interact resulting in enhanced negative impacts.

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For millennia, river mouths and estuaries have been population centers, with some of the world's greatest civilizations developing near the estuaries of the Tigris-Euphrates, Nile, Indus, and Yangtze rivers (Day et al. 1989). The protected access to abundant aquatic food resources and efficient transport of supplies and people over water has spurred the continued relationship between human cities and estuarine ecosystems. Today, many of the world's largest cities are located next to estuaries, including London, New York, Cairo, Calcutta, and Shanghai (Day et al. 1989). In addition to their cultural and economic importance, estuaries and wetlands are critical to many ecological processes important both to services humans depend upon and critical functions necessary for the continued persistence of a range of interconnected ecosystems. Production in estuaries provides needed biomass and food resources to nearby terrestrial and coastal ecosystems (Ben-David et al. 1998; Deegan et al. 2000; Bilby et al. 2003; Darimont et al. 2003). Estuarine vegetation, e.g. marshes and seagrasses, naturally purify water and stabilize coastlines (Day et al. 1989), providing protection from storm surges, floods, and hurricanes to inland terrestrial habitats (Farber 1987). Estuaries are critical nursery habitats for many economically important fisheries species (Deegan et al. 2000; Beck et al. 2001).

There has been a continued and persistent population increase in coastal areas. For example, coastal counties make up only 17% of the continental United States' land area but in 2003 were home to 153 million people, 53% percent of the nation's population (Crossett et al. 2004). This is an increase of 33 million people since 1980 (Crossett et al. 2004). Increasing population pressure on coastal ecosystems results in myriad human impacts that threaten the continued delivery of ecosystem functions and services. Overexploitation has lead to the collapse of coastal fisheries worldwide (Pauly et al. 2005). Eutrophication has resulted in toxic algal blooms and anoxic zones that kill fish and endanger the health of coastal human populations (Horner et al. 1997). Pollution can bioaccumulate in higher trophic levels, reducing the overall health and reproductive output of these species (Lam et al. 2005). Direct habitat modification, either through the diversion of water, construction and addition of structures, or dredging can kill local populations as well as alter the dynamics of water flow through the system. The alteration of hydrology in turn changes the availability of water bound resources throughout the system. Last but not least, humans intentionally and unintentionally introduce non-native animals and plants to estuaries through a variety of mechanisms. Some non-native species increase in abundance and negatively impact native species through predation (Wiles et al. 2003), competition (Byers 2000), or habitat modification (Crooks and Khim 1999). Non-native species can also harm human economic interests in estuaries by fouling structures and overgrowing or preying upon harvested species (Leung et al. 2002).

These myriad anthropogenic disturbances are damaging enough when considered on an individual basis. However, some anthropogenic disturbances may interact in a multiplicative manner (Millennium Ecosystem Assessment 2005). Given that disturbances can interact in manners that enhance impacts (Millennium Ecosystem Assessment 2005), the combination of multiple anthropogenic disturbances on estuarine ecosystems could be even more damaging than the additive impact of many individual disturbances. This dissertation explores the role and possible interaction of two human disturbances on species distribution and community composition within Elkhorn Slough, a central Californian estuary. I focus on two disturbances impacting most estuaries: anthropogenic habitat modification and the introduction of non-native species. I examine whether direct anthropogenic habitat modification and structural addition increase the spatial extent of non-native species, as well as if structure creating non-native species enhance the abundance of other non-native species associating with their biogenic structure.

Estuaries and river mouths are relatively low flow depositional environments, where soft sediments are the dominant substrate type (McLusky and Elliott 2004). As such, hard substrate and complex structural resources can often be limited in these environments, especially on the west coast of North America, where native reef-building oysters are rare. I hypothesize that the addition of hard substrates and complex three-dimensional structures will provide habitat for non-native species, increasing their local abundance and spatial extent within estuaries. Hard substrates and complex structures can be added to estuarine environments through two primary mechanisms: 1) direct anthropogenic structural additions, such as the construction of bridges, docks, tidal gates, sea walls, and breakwaters; and 2) the introduction of non-native species that form structural habitats.

Anthropogenic substrates are often constructed of artificial materials not found in the natural environment (i.e., metal, plastics, concrete, and Styrofoam). Construction materials, such as wood, which may occur naturally, are chemically treated for preservation and to prevent the attachment of organisms. Additionally, anthropogenic structures are often oriented in the water column in unnatural ways. Floating docks move up and down with the tides, effectively remaining at the same tidal level continuously. Pilings provide a continuous smooth column of substrate connecting the subtidal to the intertidal without any crevices for prey to hide. It has been shown repeatedly that anthropogenic substrates harbor distinct assemblages from those on nearby natural hard substrates (Holloway and Connell 2002; Chapman and Bulleri 2003; Wasson et al. 2005). The increase in these novel substrates could change the types of communities found in estuaries. To further complicate matters, many estuaries and harbors are highly invaded (Carlton 1979; Ruiz et al. 2000). Some of the most common vectors of human-mediated species introduction, such as aquaculture of non-native bivalves and boat hull fouling, may select for an assemblage of non-native species which can utilize anthropogenic substrates (Carlton 1979; Wasson et al. 2005).

Some non-native species can create their own structural habitat, which in turn can be utilized by native and non-native species. Species whose bodies create structural habitats are called ecosystem engineers or foundation species (Dayton 1972; Jones et al. 1994; Ellison et al. 2005). Introductions of non-native ecosystem engineers can have dramatic effects on local communities, changing species composition as well as promoting the establishment and increased impact of other associated non-native species (Ricciardi et al. 1997; Schwindt 2001; Houlahan and Findlay 2004; Neira et al. *in press*). This and other facilitative interactions between non-native species resulting in increased abundances or impacts of at least one of the non-native species involved in the interaction, is know as invasional meltdown (Simberloft and Von Holle 1999). Additionally, many non-native ecosystem engineers are fouling species, permanently attaching to hard substrates (e.g. the oysters *Crassostrea virginica* and *C. gigas*, the zebra mussel, *Dreissena polymorpha,* the kelp *Undaria pinnatifida,* the tubeworm *Ficopomatus enigmaticus,* and the bryozoan *Watersipora subtorquata*). Hard substrates may provide needed attachment sites for introduced ecosystem engineers, promoting the establishment and persistence of not only the non-native foundation species but an increase in biogenic structural habitats. The increase in non-native biogenic habitat may in turn provide habitat for other non-native species capable of utilizing the structural resources.

In the following chapters, I address four key roles of novel habitats in community structure and development. Chapter 1 focuses on what characteristics of anthropogenic structures predict the distribution of native and non-native fouling species. Chapter 2 examines the development of fouling communities under different environmental conditions throughout Elkhorn Slough. Chapters 3 and 4 examine the types of species that associate with native and non-native biogenic habitats and the impact of a non-native reef-building polychaete on species living in nearby mudflat environments.

In chapter 1, I explore the role of a variety of environmental variables in explaining the distribution of native and non-native fouling species. Through a combination of surveys, long-term water monitoring data, and experimental substrate deployments, I show that hard substrate variety and stability/size are important predictors of native and non-native fouling species presence. Surprisingly, proximity to the harbor, the location of many species introductions, as well as water variables such as salinity and nitrogen loading do not explain much of the variation in species distribution patterns. Even after considering all of the measured environmental variables, the largest quantity of variation in surveyed species distributions was explained by location within Elkhorn Slough. Location is a proxy for some unmeasured abiotic or biotic factor (such as pollution concentrations, predation pressure, or recruitment) that varies between locations. Some species were only found on anthropogenic hard substrates, indicating that species distributions may be expanded due to this human disturbance.

In chapter 2, I focus on how fouling communities develop throughout Elkhorn Slough. By following the development of assemblages on ten sets of experimental recruitment plates, I seek to describe patterns of fouling community development in this highly invaded estuary. I explore the effect of differing environmental conditions; variation in timing of substrate availability; and variation in local communities, which may act as source populations, on developing fouling assemblages. Most of the developing communities are dominated by short-lived ephemeral species, with longer-lived bivalve species never dominating any of the plate assemblages. Recruitment limitation and fluctuating environmental parameters, such as salinity, influence developing fouling communities at most sites, while competitive biotic interactions only structure developing assemblages at a few locations. As in chapter 1, unmeasured biotic and abiotic factors, which vary between sites, influence fouling assemblages' structure as well as processes controlling the development of the assemblages.

Chapter 3 examines the role of non-native biogenic habitats in providing living space for associated invertebrates as well as the impact of complex structure on local mudflat communities. I show that the tubeworm reefs of *Ficopomatus enigmaticus* provide a complex structural habitat utilized by an assemblage dominated by non-native amphipods and polychaete worms. The reefs also impact the local mudflat community, both changing assemblage structure and decreasing infaunal abundance in the mudflat directly under and around the reefs.

The finding of highly abundant non-native assemblages associated with the non-native reefs in chapter 3 motivated the habitat comparison in chapter 4. In this chapter I ask whether abundant, predominantly non-native assemblages occur in other structurally complex biogenic habitats within Elkhorn Slough, or whether the assemblage associated with *F. enigmaticus* is unique to this non-native ecosystem engineer. To address this question, I compared the assemblages associated with *F. enigmaticus* to those associating with the native oyster, *Ostrea conchaphila*, the only other hard complex biogenic habitat in Elkhorn Slough. I found that common non-native species were more abundant in the non-native habitat, even when the percentage of non-natives associated with each habitat was similar. In contrast, variation in native species abundance and identity was explained more by location within Elkhorn Slough than biogenic habitat type. This suggests that native species are adapted to specific abiotic parameters found at certain locations within Elkhorn Slough and select habitat based on the abiotic parameters not on the microhabitat provided by a particular ecosystem engineer. In contrast, non-natives may be tolerant of a wider range of abiotic parameters, but highly selective for microhabitats.

This dissertation shows that the addition of novel habitats alters community structure. The anthropogenic disturbance of substrate addition, either through human construction or species introduction, increases the spatial extent and abundance of associated non-native species in this soft-sediment estuary, demonstrating how two human disturbances can interact with one another resulting in enhanced negative impacts. Additionally, the introduction of the non-native reef building polychaete *Ficopomatus enigmaticus* represents a mechanism for "invasional meltdown", whereby facilitative interactions between two or more non-native species enhance one another's abundance or impacts (Simberloft and Von Holle 1999). Through habitat provision, non-native reefs facilitate associated non-native amphipods and polychaete worms. The interaction between associated non-native species and novel structural habitats suggests that by controlling the distribution of hard substrates in this and other estuaries the distribution and spatial extent of associated non-native species may be managed. However, ecologically important native species, such as mussels and oysters, also utilize these novel habitats. Management should also focus on native habitat restoration to promote the continued persistence of native species, while simultaneously controlling the extent of non-native biogenic habitats and anthropogenic structural additions.

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-CHAPTER ONE-

Environmental predictions of distribution and abundance of estuarine species: a comparison of natives and non-natives on hard substrates

ABSTRACT

Increasing numbers of non-native species are reported in estuaries worldwide. Many estuaries are historically soft-sediment environments, but have since undergone extensive anthropogenic alterations, increasing the availability of hard substrates (e. g. construction of bridges, jetties, and harbors). Additionally, many common vectors of marine species introductions (oyster culture, ship fouling) select for species that utilize hard substrates, leaving modified estuaries vulnerable to non-native establishment. To identify what aspects of hard substrates and the local environmental control the distribution of fouling native and non-native species, we deployed experimental substrates, used long-term data sets, and surveyed the location and abundance of five non-natives (*Botrylloides violaceus*, *Ficopomatus enigmaticus, Watersipora subtorquata*, *Bugula neritina*, *Caulacanthus ustulatus*), one native (*Ostrea conchaphila*), and the morphologically indistinguishable native and non-native species complex (*Mytilus galloprovincialis* and *M. trossulus*) in Elkhorn Slough, California. The distributions of native and non-native fouling species are controlled by similar environmental variables. Location within the estuary and characteristics of hard substrate, including variety of types and presence of low intertidal permanent structures, predicted fouling species distributions when analyzed as a group (RDA) or individually (logistic regression). In contrast, hard substrate surface area and the presence of boat access facilities were not significant predictors of species' presence which implies that non-natives are not localized to areas with fouled boats, a major vector of non-native introduction to Elkhorn Slough. Experimental additions of substrate showed that species can spread into areas without established adult populations. Species diversity and composition of assemblages that recruited to experimental surfaces did not depend on substrate type. Additionally, similar numbers of non-native species recruited to artificial

and biogenic substrates. The grouping of species into native and non-native categories, while important for management strategies, does not provide predictive understanding of species distribution and recruitment patterns. Rather management may have to proceed on a species by species basis.

INTRODUCTION

There are three distinct phases to the successful invasion by non-native species. The introduction phase occurs when organisms are transported by humans across a major geographic barrier (Richardson et al. 2000). The establishment phase is when non-native species become naturalized to the recipient system, i.e. when abiotic and biotic barriers to regular reproduction are overcome and the population is able to sustain itself from generation to generation without the need for further introductions (Richardson et al. 2000). The final phase is spread, during which naturalized organisms produce reproductively viable offspring in areas distant (100s of meters) from their initial sites of introduction (Richardson et al. 2000). Most applied marine invasion studies have focused on the arrival of non-native species into a region and the vectors leading to these introductions because this is where large-scale management efforts can have the greatest effect (Olin 1996; Carlton 1999a, 1999b; Mack et al. 2000; Kolar and Lodge 2001). There has also been a great deal of study on the establishment of non-native species both in terms of species characteristics and parameters of the recipient environment that enhance or reduce establishment potential (Robinson et al. 1995; Planty-Tabacchi et al. 1996; Stachowicz et al. 1999; Mack et al. 2000; Lyons and Schwartz 2001). Much less work has been done on the spread and local distribution of non-native species once they have established in a recipient region (but see Callaway and Josselyn 1992, Suarez et al 2001, Minchinton and Bertness 2003, Ayres et al. 2004). Yet it is at this local scale where much management is conducted. Managers of protected areas, national parks, and reserves have the ability to effect control over their management areas and frequently try to foster conditions that favor native species over non-natives. To achieve this conservation agenda, managers need to understand the processes controlling native and non-native distributions on a local scale.

There are a number of pre-settlement and post-settlement factors that have repeatedly been shown to influence species distributions. Pre-settlement processes affect the transport and supply of propagules to a particular location as well as the availability of habitat for successful settlement. Post-settlement processes (such as competition and facilitation, predation, and mortality due to abiotic factors) affect the development of settled organisms into recruits, juveniles, and eventually adults. However non-native and native species may experience different controls over these different settlement phases. For example, the source and quantity of non-native propagules may be tied to introduction vectors such that non-native populations radiate out from their sites of initial introduction within the recipient system (Elton 1958). Additionally, human disturbances may result in increased post-settlement mortality in native species while simultaneously opening up space for successful recruitment of opportunistic non-native species (Davis et al. 2000; Marchetti et al. 2004). Furthermore, recruitment limitation might be a factor in newly established non-native populations whereas abundant native populations may not experience this limitation. Understanding the difference between factors controlling native and non-native distributions may allow for the successful management of communities at the local scale of most preserves.

Northwest Pacific estuaries are particularly good systems in which to examine hypotheses about the environmental factors affecting the distribution of native and non-native species. Northwest Pacific estuaries are frequently small systems separated from one another by large expanses of high-energy open coast, making them almost island-like in their isolation from each other (Daehler and Strong 1996; Emmett et al. 2000). As such, many Northwest Pacific estuaries can be managed as individual systems. Due to the high-energy nature of most of the coast, many of the region's harbors are located in estuaries. Along with the harbors come physical and chemical human disturbances that may affect native population distributions while simultaneously introducing vast numbers of non-native species through shipping and boat traffic (Carlton 1979).

Using a central California estuary, Elkhorn Slough, as a model system we test hypotheses about environmental and anthropogenic factors influencing the distribution of native and non-native species, with the goal of providing insight for management of this and other similar systems. Many anthropogenic impacts, such as construction of structures and the restriction of flow, can impact species distributions. Through various permitting processes, management has control over these construction projects. If human impacts are identified as promoting non-native species, then these impacts may be mitigated or controlled through management processes. We will focus on hard substrate species, because of their ease of sampling, as well as the fact that one of the major human alterations to estuaries is the addition of artificial structures such as harbors, docks, and bridges, which has been shown to influence community structure and provide habitat for predominantly non-native fouling communities (Connell 2000; Davis et al. 2002; Chapman 2003).

By conducting a survey of the location of 7 focal species, deploying experimental recruitment substrates, and using long-term water monitoring data we will test the following hypotheses about environmental factors influencing the distribution of native and non-native species in Elkhorn Slough. 1) Non-native species introduced by boat traffic will decline as a function of distance from the harbor. Native species are not expected to show this pattern because they were not transported into the system by boat traffic. 2) Native and non-native fouling species will be positively correlated with the amount of hard substrate at a given location. 3) Non-native species will be more abundant on artificial versus natural hard substrates with the opposite observed for native species. Studies in Australia and California have shown that anthropogenic structures are functionally different than local rocky reefs due to material composition as well as surface orientation; supporting distinct community assemblages, frequently with abundant non-natives (Glasby and Connell 1999; Connell 2000; Glasby 2000; Chapman 2003). 4) Non-native species will be more prevalent in freshwater-influenced portions of the estuary than natives. Western Pacific species have had relatively little time (less than 10,000 years) to evolve tolerances to low salinity conditions because of the relative youth of most of the western Pacific estuaries (Emmett et al. 2000). Many non-native species from areas with much older estuaries have had more time to evolve low salinity tolerances and may be better suited to low salinity environments (Carlton 1979).

METHODS

Study System

Elkhorn Slough is a central Californian estuary (36º48.6N, 121º47.1W) 150 km south of San Francisco Bay (Fig. 1.1). The main channel of the Slough is about 11 km long with an average depth of 1.4 meters (Caffrey et al. 2002). A flooded river valley, Elkhorn Slough is primarily a soft sediment environment with the mid and low intertidal zones comprised primarily of mudflats and the high intertidal zone occupied by the pickleweed *Salicornia virginica* (Schwartz 2002). Evidence from historical maps and photos as well as geological cores indicates that Elkhorn Slough has primarily been influenced by salt water with only isolated locations and temporal periods showing evidence of communities dependent on low salinities (Van Dyke and Wasson 2005). There is no international shipping in this estuary; however there is a harbor at the mouth of the system with fishing, recreational, and research vessels in residence. Most of the wetlands of Elkhorn Slough are managed by public or state agencies including Elkhorn Slough National Estuarine Research Reserve (ESNERR).

Four to ten thousand years ago Elkhorn Slough's primary hard substrate was extremely limited, consisting mostly of shell debris and presumably drift wood (sediment core data; Hornberger 1991). Evidence from Native American middens shows that bay mussels and to a limited extent native oysters were present in Elkhorn Slough (Jones 1996; 2002). Currently, bay mussels are common but native oysters are rare in the system and the dominant biotic habitat in the system is generated by non-native species such as the reef-building tubeworm *Ficopomatus enigmaticus*. Anthropogenic hard substrates are abundant in Elkhorn Slough today, including bridges, jetties, harbors, docks, rip rap, and gravel as well as abandoned oyster culture racks and other discarded structures. In 1946 the Army Corps of Engineers cut a new mouth for Elkhorn Slough to construct Moss Landing Harbor (Gordon 1996) (Fig. 1.1). Tidal influence and water exchange have greatly increased in Elkhorn Slough due to the creation of the new mouth and the restoration of salt water flow to several intertidal marshes, resulting in increased erosion and the transformation of many intertidal mudflats into steeply eroded banks (Caffrey and Broenkow 2002, Van Dyke and

Wasson 2005). The increased erosion has exposed once-buried shell beds and the clay/peat layer, both possible hard substrate resources for invertebrates and algae.

There are 58 known marine non-native species in Elkhorn Slough, 52 of which are also found in San Francisco Bay (Wasson et al. 2001, Wasson et al. 2005). Larval dispersal of non-native species from San Francisco Bay to Elkhorn Slough is probably a minor vector of introduction when compared to the main vectors: ongoing intraregional transport by small boats between Elkhorn Slough and San Francisco Bay and the oyster culture industry, active from 1910 to the 1970s (Wasson et al. 2001). Partly due to the dominance of these introduction vectors, a majority of Elkhorn Slough non-natives (36/58) utilize hard substrates as attachment sites or crevices for protection from predators or the abiotic stressors (Wasson et al. 2001, Carlton 1979).

Survey methods and focal species

To test whether the extent and type of anthropogenic hard substrates explains the distribution of fouling non-native species in Elkhorn Slough we surveyed the distribution and abundance of five easily recognizable intertidal non-native species in 2003 (the colonial ascidian *Botrylloides violaceus*; the serpulid polychaete *F. enigmaticus*; the bryozoan *Watersipora subtorquata;* the bryozoan *Bugula neritina*; and red alga *Caulacanthus ustulatus* which for this paper will be considered cryptogenic (a species of unknown origin; (Carlton 1996) (P. Gabrielson, personal communication). These five surveyed species represent the most abundant non-native intertidal fouling organisms in Elkhorn Slough. The thirty-one other non-natives with the ability to use or associate with hard substrates are small, difficult to identify and/or sparsely distributed requiring substantially different survey methods than the visual surveys we conducted. Species were chosen to cover a diverse range of taxonomic groups and life history traits. All species were easily identifiable in the field and were of concern to the ESNERR managers because of potential impacts, increasing abundances, and possible spread.

To identify whether the same environmental factors controlling non-native distributions were also responsible for fouling native species distributions we surveyed the location and abundance of two of the primary native fouling species in Elkhorn

Slough in 2003, the native oyster *Ostrea conchaphila* and the bay mussel (a morphologically indistinguishable species complex of the non-native *Mytilus galloprovincialis*, the native *Mytilus trossulus*, and their hybrids, which are all found in Elkhorn Slough (Braby and Somero 2006).

Surveys were conducted by foot and by motorboat during low tides. A site was defined as a 50-100 m stretch of the shore chosen to cover the full extent of the habitats along both banks of Elkhorn Slough's main channel. Sites were 20 m - 50 m stretches of the intertidal, encompassing distinct habitats along the shore. The presence and abundance of the non-native species were visually estimated on a 0-4 scale, with 0 = not present, 1 = ≤ 1%, 2 = 1-10%, 3 = 11-50%, and 4 = ≥ 50% of the available surface area at a site occupied by a given non-native species. For species found exclusively on hard substrates, the available surface area was determined as the total hard substrate in the intertidal zone at a given site. For species that could also occupy mudflats, the available surface area was all of the intertidal mudflats and hard substrate at a given site. We closely inspected the hard substrates and mudflats to ensure we were not missing cryptic populations of the focal species (e.g. those occupying crevices).

The location of each site was recorded with a handheld GPS, the colonized substrate type and surrounding habitat types were noted, and the habitat and species were photographed. The amount of each hard substrate type in the intertidal zone was visually estimated in square meters and was categorized as anthropogenic (e.g. wooden bridge pilings, concrete, Styrofoam, rubber) or natural (e.g. peat, shell fragments, driftwood) (Table 1.1). Because the location of substrate within a site (e.g. tidal zone and height above the mudflat) may influence which species survive at the site, we also created a categorical variable called "good substrate". We defined good substrate as permanent, stable, low intertidal substrate of at least 0.5 m^2 in area. Sites were categorized as having or not having good substrate. We surveyed 125 sites in July 2003.

Environmental data

To examine how local environmental conditions influence the distribution of fouling native and non-native species, we assembled monitoring data provided by

ESNERR. Five water variables were measured at each of 4 reserve-maintained and 24 volunteer water-monitoring stations: temperature, salinity, dissolved oxygen (mg/L), pH, and turbidity (Table 1.1). Reserve maintained stations have YSI 6600upg® data loggers which take measurements every 30 minutes and have been gathering data for 1–4 years. The volunteer water data were gathered once a month for up to 10 years, most recently using a portable YSI 6600® data logger. Water data were mapped onto Elkhorn Slough Arcview base maps as observation points which were then used to create raster layers through an inverse distance weighted (IDW) extrapolation process within the ArcGIS 8.2® software (McCoy and Johnston 2001). We took into consideration the hydrology of Elkhorn Slough during the extrapolation process. Areas with reduced tidal flow were only compared to nearby muted flow lagoons and main channel locations were only extrapolated from other main channel sites. The extrapolation of water variables to areas that were not directly measured allowed us to estimate water values for each survey site. We calculated the dry season (May through October) and wet season (November through April; (Conomos et al. 1985) minimum, maximum and mean for temperature, salinity, dissolved oxygen, pH, and turbidity across all years resulting in thirty water variables used in subsequent analysis.

A boat access variable was created to account for the presence of boat launch/ docking facilities because the movement of fouled boats into the slough is one of the main vectors of invasion transport (Table 1.1). A variable to account for distance from the mouth of Elkhorn Slough was also included, because even though Elkhorn Slough does not have a strong estuarine gradient, there are a number of variables which could influence species distribution that can change with distance from mouth, such as availability of ocean-derived food resources and predators. Geo-referenced survey data were mapped onto Arcview base maps of Elkhorn Slough's wetlands and water channels provided by ESNERR. Site locations were plotted as points on the base maps and distance from the mouth of Elkhorn Slough was measured as the distance from the surveyed point to the mouth through existing water channels.

Substrate experiment

To determine if there is a difference in the development of fouling communities on anthropogenic and natural hard substrates, five experimental substrates (native oyster shell, dead and cleaned *F. enigmaticus* clumps, wood, rock, and PVC) representing some of Elkhorn Slough's most abundant natural and anthropogenic hard substrates, were deployed at six intertidal sites (triangles in Fig. 1.1). Oyster shells and granite rocks were collected from Elkhorn Slough, scrubbed clean with steel wool, to remove any colonizing organism and rinsed under fresh water. *F. enigmaticus* clumps were collected from Elkhorn Slough, allowed to dry for three weeks to kill the tubeworms and any associated organisms, and then repeatedly rinsed under fast flowing fresh water and submerged for three days to remove soft tissue. Untreated 2 x 4 pine planks were cut into 10 cm lengths. PVC panels were cut into 5 x 10 cm pieces, covered with 3M™ Safety-Walk™ to add rugosity and enhance recruitment. Each substrate was approximately 10 cm high by 5 cm wide. Two replicates of each substrate type were attached with Z-spar© saltwater epoxy to PVC frames such that they faced vertically into the water column and were 15 cm above the soft sediment benthos. Frames were submerged in saltwater flow-through tanks for two weeks prior to deployment in the field to allow chemical contaminants to seep out and the beginning of a biofilm to develop. Substrates were deployed at 0 ft MLLW in May 2003 and retrieved in October 2004. All organisms attached to the substrates were identified under a dissecting microscope to the lowest taxonomic level possible.

To determine if the species recruiting to the experimental substrates were also found in the local environment, twice during the deployment period (July 2003 and January 2004), we surveyed the fouling organisms within a 20 m radius of the experimental recruitment substrates. We identified all species attached to hard substrates greater than 5 mm in length and categorized their abundance in the local environment with the same 0 - 4 scale described above.

Data analysis

To identify which local environmental factors and characteristics of hard substrates explain part of the observed non-native and native species distribution patterns, we conducted two Redundancy Analyses (RDA) using the survey and environmental data. In RDA, values for the explanatory variables are constrained to be linear combinations of measured environmental variables. The response variables were the seven surveyed species distributions and abundances. The explanatory variables were the environmental variables: distribution of natural and anthropogenic hard substrates, presence of good hard substrates, boat access, and extrapolated wet and dry season water variables. The first RDA was conducted using all sites and all environmental and species variables discussed above with distance from mouth included as an environmental variable. The second RDA was the same as the first except distance from mouth was used as a covariable not an explanatory variable, allowing the effect of the environmental variables to be considered after the effect of location had been taken into account. In each RDA, all environmental variables were added to the model to determine the total explainable variance. The contribution of individual environmental variables was then determined with a forward selection RDA which adds environmental variables one at a time to the model based on their linear regression fits, until all significant contributors were included (Lepš & Šmilauer 2003). Monte Carlo permutation tests assessed the significance of all environmental variables in the model (ter Braak and Šmilauer 2002). For all RDAs we focused on inter-species correlations.

To determine which, if any, environmental factors were significant predictors of individual species distribution patterns we conducted 7 separate stepwise polytomous logistic regressions, one for each surveyed species. Logistic regressions were necessary because of the categorical abundance information we collected. Only individually significant variables (at the 0.10 level) were added through a forward stepwise analysis to each species' model (Sokal and Rohlf 1995). We present our results as odds ratios. The odds of the response are given by p/(1-p), where p is the probability of response, and the odds ratio is the multiplicative factor by which the odds change when the independent variable increases by one unit (in our case going from 0 = not present to 1 = trace presence for example).

To determine if more fouling species successfully recruited to one experimental hard substrate over another, we compared the number of species growing on each experimental substrate using a single fixed factor (substrate type) ANOVA with five levels (oyster shell, *F. enigmaticus* clump, rock, wood, and PVC). Sites were considered replicates (n = 6) and number of species/substrate type the response variable. Additionally, we used two 1-way analysis of similarity (ANOSIM) in the Primer V5.2© software to test for the effects of site and substrate type on patterns of fouling community composition (Clarke and Warwick 1994). To determine if species recruitment success was dependent on the presence of species in the local environment we tabulated how frequently each species was a) found on recruitment substrate and in the local environment, b) found on recruitment substrate but not in the local environment, c) found in the local environment but not on recruitment substrate, or d) not found on recruitment substrate or in the local environment. We then summed these values across all species and conducted a Chi-squared contingency test. We also tabulated the number of times a species occurred on each substrate type to identify patterns of individual species preferences, which may have been overlooked in the ANOVA and ANOSIM analyses, which take into consideration the entire community and not individual species.

RESULTS

The seven surveyed species in Elkhorn Slough vary in their abundance and distribution patterns. The bay mussels were the most widely distributed species in Elkhorn Slough, found at 46 of the 125 survey sites (Fig. 1.2a), followed by the cryptogenic red alga *Caulacanthus ustulatus* found at 35 sites. The rarest surveyed species were the non-native colonial ascidian *Botrylloides violaceus* (15 / 125 sites), the native oyster *Ostrea conchaphila* (21 / 125 sites), and the non-native bryozoan *Bugula neritina* (21 / 125 sites). The non-native serpulid polychaete *Ficopomatus enigmaticus,* reached the highest local densities, covering an average of 30% of the available substrate at sites where it was found. *F. enigmaticus* and *O. conchaphila* were primarily found in the upper slough, with dense populations in the distal northern end of the system (Fig. 1.2a, b). *B. neritina,* and *B. violaceus* were found throughout Elkhorn Slough except in the northernmost areas (Fig. 1.2f, g). The bay mussels, the bryozoan *W. subtorquata*, and the alga *C. ustulatus* had their highest densities at two distinct locations: in the main channel near the harbor and near Kirby Park (Fig. 1.2c, d, e).

Anthropogenic hard substrates accounted for 85% (nearly 3,300 m^2) of the total hard substrate at the surveyed sites, whereas only 15% (580 m^2) were natural hard substrates, 403 m^2 of which are exposed peat and the rest roots and shells (see Table 1.1 for a list and categorization of observed hard substrates). “Good substrates” (permanent, stable, low intertidal substrate at least 0.5 m^2) were found at 61 out of the 125 surveyed sites.

The results from the first RDA showed that distance from mouth has the greatest explanatory value among the environmental variables considered, accounting for 21% of the variability in species distributions. A total of 58% of the variability was accounted for by all environmental variables (eigenvalue 0.579). The effect of distance from mouth reflects the fact that species tended to occur in the upper or lower part of the slough. The second RDA, with distance from mouth as the covariable, allowed us to examine the influence of other environmental variables once location was taken into consideration. Thirty-seven percent of the variance in species distributions was explained by the remaining environmental variables (eigenvalue = 0.373, Table 1.2). Forward selection RDA determined that three of these variables were individually significant contributors to the model: number of hard substrate types explained 8% of the variance in species distributions, followed by turbidity (wet season mean; 5%), and the presence of “good” substrates (3%) (Table 1.2). All species were positively correlated with the total number of hard substrate types, with *B. neritina, W. subtorquata,* and *O. conchaphila* having the highest correlation, and the bay mussel complex having only a slight trend toward positive correlation (Fig. 1.3). The presence of “good” hard substrates, regardless of their type or diversity, was also positively correlated with the distribution of most of the surveyed species, especially bay mussels and *F. enigmaticus*. However, “good” hard substrates at a site were not correlated with the distribution of *B. violaceus* and only slightly positively correlated with the distribution of *C. ustulatus* (Fig. 1.3). *C. ustulatus* and *B. violaceus* were found growing on exposed peat (at 37% and 40% of the sites occupied, respectively) whereas *F. enigmaticus* was never observed on or associated with natural hard substrates, but was observed on wood pilings at 63% of the sites where it was found. Turbidity (wet season mean) was correlated with the distribution of bay mussels and *F. enigmaticus* (Fig. 1.3).

Salinity (dry season mean) was almost significant in the forward selection RDA, explaining 2% of observed species distribution patterns (Table 1.2). Interestingly, neither the amount of anthropogenic or natural hard substrates nor boat access were significant explanatory variables in either of the RDAs (Table 1.2).

Single species logistic regressions found significant explanatory environmental variables for 5 out of the 7 species. The presence of wood increased the probability of bay mussels occurring at a given site (significant odds ratio (0.809) for moving from group 0 (not present) to group 1 (trace presence); with a full model chi-squared = 40.328, df = 8, McFadden's R^2 = 0.149; Table 1.3a). The probability of *B. neritina* occurring at a site is negatively correlated with the presence of roots (significant odds ratio (0.376) for moving from group 0 (not present) to group 1 (trace presence); with McFadden's R^2 = -0.206; Table 1.3b). The odds of increasing the abundance of *F. enigmaticus* are enhanced with increasing distance from the mouth of Elkhorn Slough (significant odds ratios for all groups; with a full model chi-squared = 93.401, df = 8, McFadden's R^2 = 0.472; Table 1.3c). The presence of concrete and brick increased the probability of *W. suborquata* occurring at a given site (significant odds ratio (0.807) for moving from group 0 (not present) to group 1 (trace presence); with a full model chi-squared = 28.549, df = 8, McFadden's R^2 = 0.121; Table 1.3d). Natural hard substrate types and peat increase the likelihood of finding *C. ustulatus* at a given site (full model chi-squared = 28.549, df = 8, McFadden's R^2 = 0.121; Table 1.3d). None of the environmental variables used in the study were significant predictors of the distribution of *O. conchaphila* or *B. violaceus*. Note that each species is correlated with a different environmental variable and most of these variables describe a type of hard substrate or some aspect of hard substrates in general. Only *F. enigmaticus* has a significant environmental variable other than a hard substrate variable (distance from mouth) in its logistic regression model.

Nineteen species colonized the experimental substrates after a 16-month deployment in the field, including the surveyed species *F. enigmaticus*, *B. neritina*, *W. subtorquata*, *C. ustulatus*, and *O. conchaphila*. *B. violaceus* and the bay mussel did not establish on any of the experimental substrates at any of the sites (Table 1.4). Eight of the species recruiting to the experimental substrates were native, 8 were non-native, and

3 were cryptogenic. Native and non-native species recruited to both the anthropogenic (PVC, rock, and wood) and biotic (*F. enigmaticus* tubes and oyster shells) substrates equally (native species: anthropogenic = 7 species (total number of species recruited across all sites), biotic = 7 species; non-native species: anthropogenic = 8 species, biotic = 7 species). PVC plates were the least frequently colonized, with only 10 species recruiting, including *Balanus glandula* and *C. ustulatus*. Wood and *F. enigmaticus* tubes were most frequently colonized, with 16 species recruiting to each substrate, including *F. enigmaticus*, the bryozoan *Amathia vidovici*, and the green alga *Ulva fenestrata*. There was no significant difference between the number of fouling species found on the five experimental substrate types when sites are used as replicates (ANOVA, F = 0.92, df = 4, 25, *p* = 0.47), but there was a trend for wood and *F. enigmaticus* tubes to have a higher average number of species recruiting/ site (Fig. 1.4). When variation in community composition among substrate types was considered through multivariate analysis, there were significant differences between locations (ANOSIM global R = 0.686, *p* = 0.001), but not between substrate types (ANOSIM global R = 0.126, *p* = 0.989). This indicates that the composition of assemblages did not differ among substrate types but rather among sites. Species recruit to experimental substrates equally regardless of whether they are found in the immediate environment or not (21 occurrences of recruited species also found in the local environment versus 20 occurrences of recruited species not found in the local environment). Less frequently, species were found at a site but did not recruit to the experimental substrate (14). There were 53 instances where a species did not occur on any recruitment substrates or at the site. The contingency table for the analysis of species occurrences at sites versus occurrence on recruitment substrates is significant (chi-square = 9.34, df = 1, *p* = 0.0022), indicating that it is more likely than chance for species not to recruit or be found at a given site.

DISCUSSION

Species do not show distinct distribution or recruitment patterns when grouped by their native or non-native status, which implies that the native versus non-native distinction, while highly important to management, does not provide insight into the mechanisms responsible for controlling where species are found within a given system. Rather, the same set of environmental variables explained significant amounts of variation in the distribution of all surveyed species, native and non-native alike. One of the most influential environmental variables explaining species distributions were aspects of hard substrate at a site. This was true when all seven species were considered as a group or when each species was analyzed separately. This is not surprising considering we surveyed fouling species. However, what was surprising was that abundance of hard substrate was not predictive but the variety of substrate types was. In seeming contradiction to the multiple species analysis, there was no difference between the number of species recruiting to each of the experimental substrates, nor did any one species recruit preferentially to any experimental substrate type. The importance of variety of types of hard substrate to the distribution of all species is most likely not due to individual species preference for a particular substrate but rather to some other aspect of the substrates such as their distribution throughout the site. Location within Elkhorn slough was also important, but water characteristics rarely influenced surveyed fouling species distribution patterns. This suggests that the relatively few water-monitoring stations were not adequate to capture important water characteristics varying along the length of the slough. Alternatively, assemblage variation along the length of the slough was determined by some unmeasured abiotic or biotic characteristics, such as pollution, propagule supply, or predator abundance. Below, I address each hypothesis providing interpretations of the presented data that lead to either accepting or rejecting a given hypothesis.

Hypothesis 1: *Non-native species introduced by boat traffic will decline as a function of distance from the harbor. Native species should not show this pattern.* There was no clear indication of invasive species consistently occurring near the harbor and decreasing in abundance with distance from this likely point of introduction. The most abundant surveyed species in the harbor was the bay mussel complex and the conspicuous non-native most likely introduced through boat fouling, *Ficopomatus enigmaticus* (Wasson et al. 2001) was never found in the harbor. The only non-native species to come close to the hypothesized pattern was *Watersipora subtorquata,* which was also probably introduced through boat fouling. One reason for this lack of pattern may be that many of the non-native species in Elkhorn Slough have more than one potential vector of introduction. For example, *Bugula neritina* and *Botrylloides violaceus* have at least two potential vectors of introduction into Elkhorn Slough: oyster culture and boat fouling. The culturing of non-native oysters occurred throughout the estuary and continued for seven decades (Wasson et al. 2001), providing ample opportunity for non-native species introductions throughout the slough. If oyster culture is indeed the vector of introduction, then the harbor is not the location of the initial population and as such would not be expected to host higher densities of non-natives such as *B. neritina* and *B. violaceus*. Even without direct inoculation of many different sites through oyster culture, our recruitment experiment provides evidence that larvae of a variety of organisms, from sponges to bryozoans and crustaceans, are transported throughout the system and can recruit successfully in locations without prior adult populations. This successful colonization of new sites occurred over the 16 months of our experiment. Since many of these species are known to been in the system since Wasson and colleagues' 1998 survey (Wasson et al. 2001) and suspected of being in Elkhorn Slough for decades, there is ample of time for these species to spread throughout this 11 km long system. Only one of the surveyed invasive species had a distribution pattern radiating out from the harbor area, even though at least four of the five species may have been introduced through boat fouling. Whereas the bay mussel had its greatest population density in the harbor, the opposite of what was hypothesized for native species. Non-native species, which were likely introduced through boat fouling, do not have a clear pattern of declining in abundance with distance from the harbor. We present two possible explanations for this lack of pattern: 1) other vectors of introduction are responsible for the non-native species' introductions or 2) enough time has passed for larval to recruit to new locations throughout the slough to obscure any pattern that may have once existed. We thus reject our first hypothesis.

Hypothesis 2: *Native and non-native fouling species will be positively correlated with the amount of hard substrate at a given location.* While surveyed fouling species' distributions were explained in part by the presence of hard substrate, the abundance of hard substrate at a given site was not predictive in the full species RDA model. Rather, the variety of different kinds of substrate and whether large low intertidal permanent substrate was present at the site were significant. When individual species were analyzed separately, four out of the five species distributions that could be modeled were explained by the distribution of a specific type of hard substrate. For example, the likelihood of *B. neritina* occurring at a site was negatively correlated with the abundance of roots at the site. In this case, *B. neritina* is not responding to the roots but rather to the fact that roots are only observed at highly eroded sites. At these sites, nearly vertical banks limit the amount of intertidal habitat on which *B. neritina* can establish. To further complicate matters, the recruitment experiment did not reveal a particular substrate with significantly more species recruitment or any individual species which consistently recruited to only one experimental substrate. These apparently contradictory results indicate that the environmental variable to which species are actually responding may not have been measured. Hard substrate types might be acting as a proxy for some other biologically important aspect of the site such as the distribution of hard substrates within the site. When many different types of hard substrate were found at a site it was frequently due to multiple structures or discarded items throughout the sites (personal observations). In contrast, abundant hard substrates were usually due to one large structure like a boat dock or a bridge with replicate or expansive similar hard substrates. It is likely that multiple types of hard substrate, which were frequently scattered throughout the site, are sampling different physical environments, as opposed to the more monotonous sampling of the environment by large expansive or replicate structures. While it is unclear what aspect of hard substrate fouling species are responding to, there is no evidence to support our hypothesis of a positive correlation with the abundance of hard substrate. We thus reject our hypothesis.

Hypothesis 3: *Non-native species will be more abundant on artificial versus natural hard substrates, with the opposite observed for native species.* Just as with the environmental variable predicting species distributions, there is no patterned response of natives versus non-natives to the added anthropogenic or naturally occurring hard substrates. Anthropogenic substrates predicted the distribution of the bay mussels species complex and non-native *W. subtorquata* in the individual species analysis. In contrast, naturally occurring substrates predicted the distribution of the non-native *B. neritina* and the cryptogenic *C. ustulatus*. Additionally, the substrates we categorized as natural are most likely enhanced due to human modification to Elkhorn Slough's hydrology and subsequent increased erosion throughout much of the system (Van Dyke and Wasson 2005). Erosion removes soft-sediments exposing once buried shell beds and peat layers. Erosion also collapses banks, and clumps of *Salicornia virginica* containing roots and peat tumble into the intertidal (personal observations). The categorization of these "natural" substrates may be more correctly described as "anthropogenically enhanced erosion exposed" hard substrates. Furthermore, recruitment of non-native species did not occur more frequently on experimental artificial substrates as compared to biotic substrates. There is no relationship between the origin of substrates and the abundance of native versus non-native species establishing on the substrate. We thus must reject our hypothesis.

Hypothesis 4: *Non-native species will be more prevalent in freshwater-influenced portions of the estuary than natives.* Salinity was not a significant predictor of surveyed species distribution when considered as a group or individually. The only water characteristic that explained part of fouling species' distribution patterns was turbidity (wet season mean). High turbidity within Elkhorn Slough's main channel is due mainly to the strong tidal exchange. Turbidity levels may control the distribution of filter-feeding animals by clogging up their feeding appendages with suspended particles. For example the surveyed tunicate, *B. violaceus*, and the bryozoans, *W. subtorquata* and *B. neritina*, which feed on small suspended particles, are more common in the less turbid central slough. In contrast, non-specific filter-feeders with the ability to sort incoming particles, such as the bay mussel, were found in the higher turbidity harbor region. However, water variables are one of the greatest sources of uncertainty in this study with sites' water variables extrapolated from relatively few monitoring stations. Although we were careful to limit extrapolations to sites with similar hydrological characteristics, it is likely that higher resolution data would have revealed a stronger influence of water quality characteristics, specifically salinity, on species distributions. For this reason, we can not accept or reject this hypothesis.

The surveyed species had different distributions with no discernable patterns separating native from non-native species groups. This implies that the environmental variables controlling non-native distributions are not unique to non-native species, but influence native distributions as well. Another possible explanation for the lack of a native/non-native pattern is that many of the surveyed species are naturally found under a broad set of environmental conditions, making it hard to identity particular environmental conditions contributing to difference in native and non-native distributions, let alone individual species distributions. Our recruitment experiment corroborates the finding of the survey, with no difference in recruitment to different substrate types when species were divided into native and non-native groups. These species divisions, while important to management planning, did not provide insight into predictable recruitment or distribution patterns. This finding makes managing the system for the benefit of native species and the detriment of non-natives challenging. However, our results do offer some management direction. For example, *Ostrea conchaphila*, a rare native species of management concern, recruited to three of the six recruitment locations. One of these locations, site D, lacks highly abundant non-native populations. Directed oyster restorations efforts in this location may succeed due to recruitment success and lack of competitive non-natives such as *F. enigmaticus*. Simultaneous with this restoration effort, an attempt could be made to limit the distribution of fouling organisms in general, throughout the system. By limiting the variety of types and spatial distribution of hard substrates, through removal of discarded items and non-functional structures, the fouling communities, which are primarily comprised of non-natives (Wasson et al. 2005), may be controlled. Further development in the system could be managed with an eye toward restricting hard substrate additions to areas already containing hard substrate, such as the harbor. In this study we show that the desirable delineation of species along native and non-native lines does not necessarily provide insight into the processes controlling distribution and recruitment within an estuary. Management based solely on a desire to promote natives and control non-natives may not be possible; instead, individual species management goals may have to be adopted and conducted simultaneously.

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Table 1.1 Environmental variables used in RDA analysis. All water variables were divided into dry (May through October) and wet seasons (November through April) (Conomos et al. 1985). The minimum, maximum, and mean values for each season were calculated. In addition to the listed variables, the quantity of each individual hard substrate was included in the RDA. SD = standard deviation.

Environmental variable	**measurements at # of sites**	**years when measurements were conducted**	**range**	**mean**	**SD**
distance from mouth (km) (the covariable)	125	2003	0.3 – 9.9	3.9	3.1
boat access (presence/absence)	125	2003	0 – 1	0.1	0.4
anthropogenic hard substrate quantity (m^2)	125	2003	0 – 200	26.3	47.6
anthropogenic hard substrate types	125	2003	0 – 4	1.2	1.0
(wood, metal, glass, sandbags/rope, plastic/PVC/rubber, styrofoam, concrete)					
natural hard substrate quantity (m^2)	125	2003	0 – 120	4.6	14.7
natural hard substrate types (peat, roots, shell)	125	2003	0 – 2	0.5	0.6
presence of good substrate (low intertidal, permanent, >0.5 m^2)	125	2003	0 – 1	0.5	0.5
Six variables per water characteristic (dry season min, max, mean and wet season min, max, mean)					
temperature (°C)	28	1992 to 2002	7.5 – 29.5	17.7	4.4
salinity (ppt)	28	1992 to 2002	0.06 – 49.2	25.1	13.0
dissolved oxygen (mg/L)	28	1992 to 2002	1.9 – 17.9	9.7	3.4
pH	28	1992 to 2002	6.3 – 9.9	8.5	0.6
turbidity (NTU)	28	1992 to 2002	0.4 – 675	47.8	73.2

Table 1.2 Results for the second RDA analysis with all sites, using distance from mouth as the covariable. Variance explained is reported as eigenvalues with percentages in parentheses. Significance values based on Dunn-Šidák corrections for multiple tests: NS $p >$ 0.0073, * $p < 0.0073$, ** $p \leq 0.002$ (Sokal and Rohlf 1981).

1st Canonical axis	eigenvalue	**0.148 (15%)**	**All Canonical axis**	eigenvalue	**0.373 (37%)**
	F ratio	19.734		F ratio	2.933
	p value	0.002		*p* value	0.002
select environmental variables		**eigenvalue**	**F ratio**	***p* value**	**significance**
total hard substrate types		0.080 (8%)	12.399	0.002	**
turbidity (wet season mean)		0.046 (5%)	7.556	0.002	**
presence of good substrate		0.030 (3%)	5.082	0.002	*
salinity (dry season minimum)		0.019 (2%)	3.312	0.014	NS
boat access		0.007	1.136	0.338	NS
natural hard substrate quantity (m^2)		0.005	0.946	0.422	NS
anthropogenic hard substrate quantity (m^2)		0.002	0.372	0.878	NS

Table 1.3 Results of single species logistic regression. *Ostrea conchaphila* and *Botrylloides violaceus* have no significant environmental predictors. Bold numbers are significant constants or environmental variables at $p = 0.10$.

A.	**Bay mussel complex**	
	constant	*wood*
Choice group	t ratio	odds ratio (upper-lower)
0 to 1	**3.104**	**0.809 (1.032-0.643)**
1 to 2	1.36	0.993 (1.016-0.971)
2 to 3	1.258	0.974 (1.01-0.939)
3 to 4	**1.912**	0.986 (1.014-0.958)
Model chi-squared (df)	**40.328 (8)**	
McFadden's R^2	0.149	

B.	***Bugula neritina***	
	constant	*roots*
Choice group	t ratio	odds ratio (upper-lower)
0 to 1	**4.271**	**0.376 (0.879-0.161)**
1 to 2	**2.704**	0.184 (4.588-0.007)
2 to 3	0.902	0.271 (27.352-0.003)
3 to 4	**1.398**	0.232 (20.389-0.003)
Model chi-squared (df)		
McFadden's R^2	-0.206	

C.	***Ficopomatus enigmaticus***	
	constant	*distance for mouth*
Choice group	t ratio	odds ratio (upper-lower)
0 to 1	**5.492**	**0.096 (0.337-0.027)**
1 to 2	**5.434**	**0.202 (0.684-0.060)**
2 to 3	**5.789**	**0.237 (0.895-0.063)**
3 to 4	6.301	**0.272 (1.199-0.062)**
Model chi-squared (df)	**93.401 (8)**	
McFadden's R^2	0.472	

D.	***Watersipora subtorquata***	
	constant	*concrete and brick*
Choice group	t ratio	odds ratio (upper-lower)
0 to 1	**6.708**	**0.807 (0.935-0.697)**
1 to 2	**2.951**	0.991 (1.013-0.969)
Model chi-squared (df)	**28.549 (8)**	
McFadden's R^2	0.121	

E.		***Caulacanthus ustulatus***	
	constant	*natural HS types*	*peat*
Choice group	t ratio	odds ratio (upper-lower)	odds ratio (upper-lower)
0 to 1	**3.958**	**0.124 (0.930-0.016)**	**0.897 (0.997-0.808)**
1 to 2	**2.805**	**0.039 (0.419-0.004)**	0.992 (1.12-0.880)
2 to 3	**2.231**	**0.083 (0.782-0.009)**	1.027 (1.088-0.969)
3 to 4	0.757	0.470 (4.733-0.047)	0.998 (1.073-0.929)
Model chi-squared (df)	**28.549 (8)**		
McFadden's R^2	0.121		

Table 1.4 Surveyed species recruitment to experimental substrates at the six deployment locations. Under each substrate is a list of all the sites from north to south. Numbers in the matrix represent the percentage of sites where a species recruited to a given substrate out of the total number of sites where the species was observed recruiting. The last series of columns summarizes the site surveys. Bold letters represent sites where the species was observed in the local environment near the plates; gray backgrounds are species that recruited to any experimental substrate. *N = native, I = introduced or non-native, and C = cryptogenic. **Site survey data report the presence of yellow sponge, not specific species of sponges.

Species	Phylum	N /I /C*	Recruitment substrates																															Site survey					
			Plate						Rock						Wood						*Ficopomatus* tubes						Oyster shell										
			A	B	C	D	F	G	A	B	C	D	F	G	A	B	C	D	F	G	A	B	C	D	F	G	A	B	C	D	F	G	A	B	C	D	F	G
Amathia vidovici	Ectoprocta	N			33						33						33				100	100	100						33				▨	▨	▨			
Balanus glandula	Crustacea	N		80	80	80		80		40				40		80		80	80	80						20		60			60	60	A	▨	C	D	F	G
Bowerbankia gracilis	Ectoprocta	I									33					33					66	66					33						▨	▨				
Bugula neritina	Ectoprocta	I								25							50	50			25												▨	▨	C	D		
Caulacanthus ustulatus	Rhodomenia	C					50				50						50						50						50					B	C	D	F	
Chthamalus sp.	Crustacea	N				100																														▨	F	
Conopeum osburni	Ectoprocta	N							33						66		66				33							66	66				A	▨	▨			
Cryptosula pallasiana	Ectoprocta	I					25											25			50	50						50					▨	▨		D		
Ectopleura crocea	Cnidaria	I			100																								100						▨			
Enteromorpha intertinalis	Chlorophyta	N					100												100						100									B			F	
Ficopomatus enigmaticus	Annelida	I							100	100					100	100					100	100					100	100					A	B	C	D	F	G
Halichondria bowerbankia	Porifera	I								50					50						100	100						50					A	B		D	**	
Haliclonia ?	Porifera	C			50						50					50							50					50					A	B	▨	D	**	
Melosira sp.	Bacillariophyta	N																					50							50					▨	▨		
Obelia sp.	Cnidaria	C					100												100						100												▨	
Ostrea conchaphila	Mollusca	N								33						66		66			66	66						66		66			A	▨	C	D		
Ulva fenestrata	Chlorophyta	N					50					100	100					100	100					100	100						50					D	F	
Watersipora subtorquata	Ectoprocta	I																50				50								50				▨		D	F	

Fig. 1.1 Elkhorn Slough, a central Californian estuary located 150 km south of San Francisco Bay, USA. Dark areas are water. Gray areas are wetlands. Triangles represent substrate experiment deployment sites lettered A, B, C, D, F, G in accordance with recruitment sites from chapter 2.

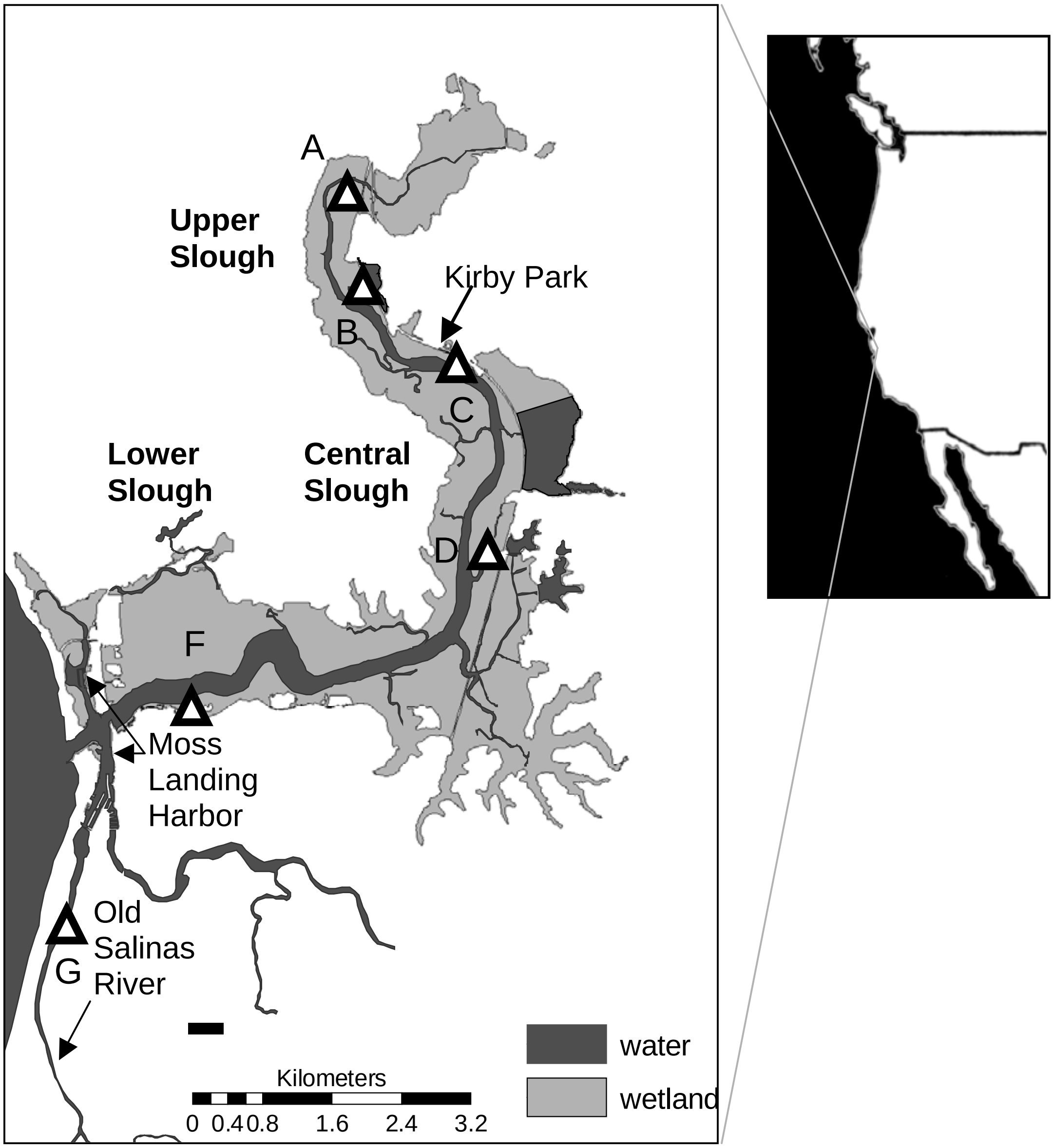


Fig. 1.2 The 2003 distribution of seven focal species surveyed in Elkhorn Slough, California. Circles are sites where focal species were observed. Small white circles are survey sites where less than 1% of the available surface area was occupied, whereas large black dots are survey sites where more than 50% of the available substrate was occupied by the surveyed species.

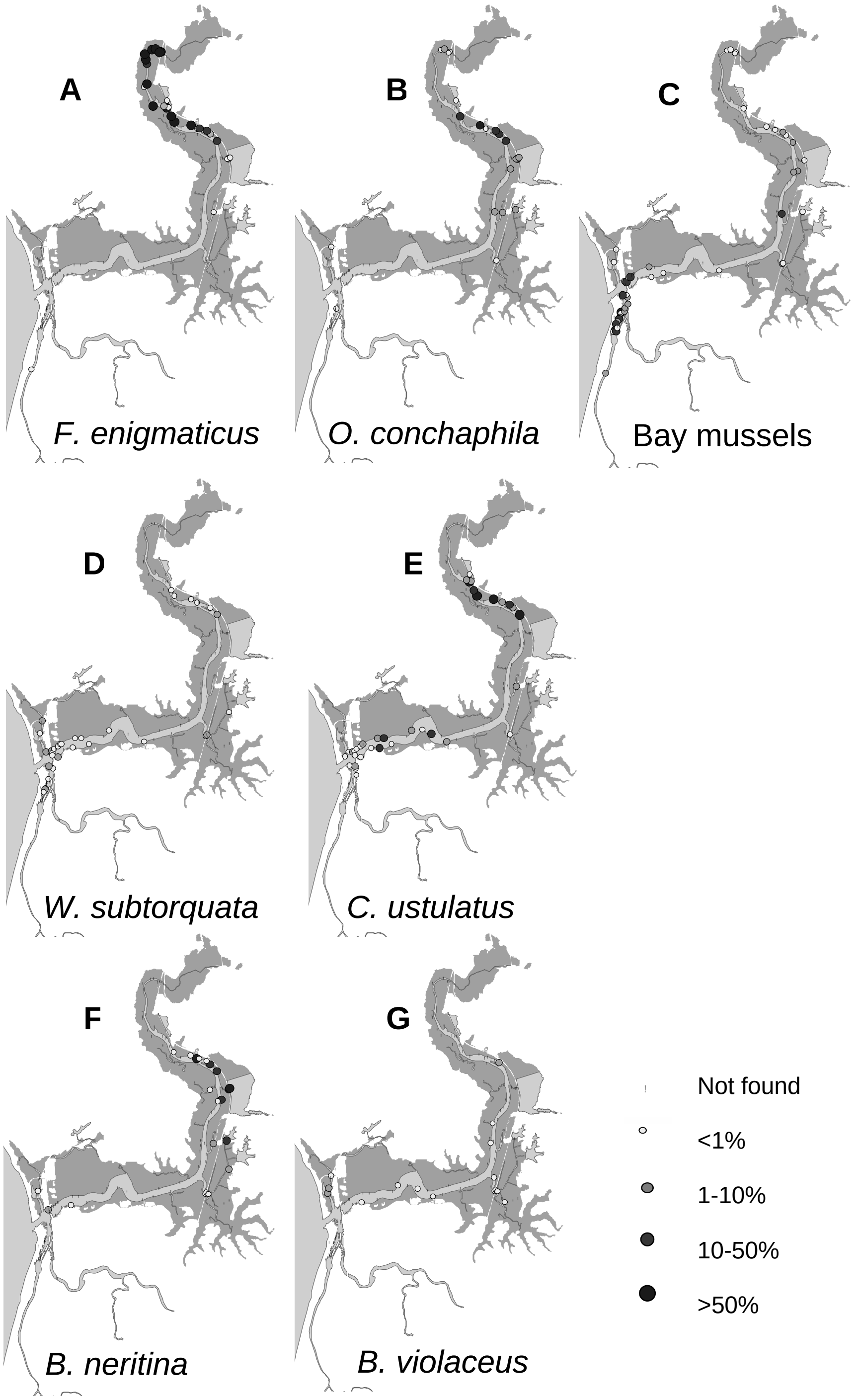


Fig. 1.3 Ordination of second RDA results with the seven surveyed species and all sites (distance from mouth was the covariable). The RDA focused on inter-species correlations. The species scores were post-transformed by dividing by their standard deviation so that the resulting lengths of species arrows express how well the ordination diagram approximates the values for each species (Lepš and Šmilauer 2003). Species arrows are black. Gray arrows represent significant environmental variables. Species arrows and environmental arrows forming obtuse angles are negatively correlated; whereas, arrows forming acute angles are positively correlated. Strength of the correlation is interpreted by a perpendicular projection of the arrow tip from one arrow to the shaft of another arrow (Lepš & Šmilauer 2003).

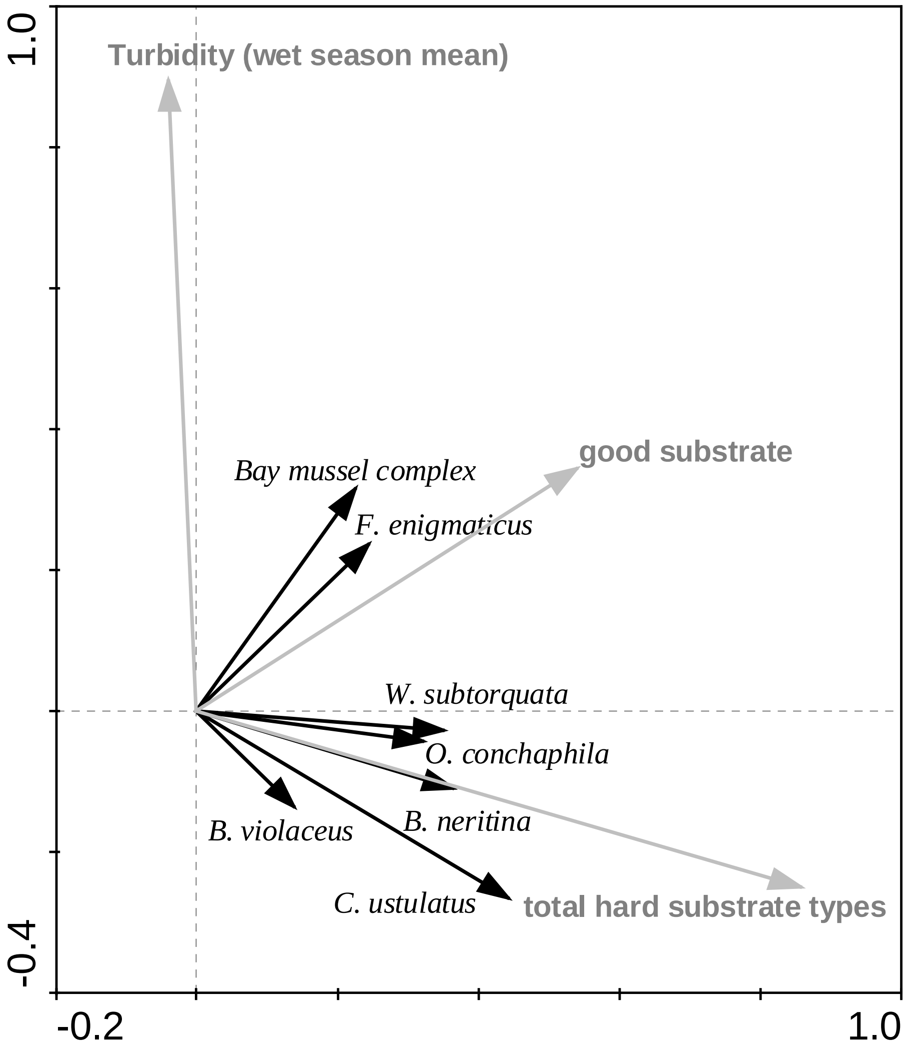
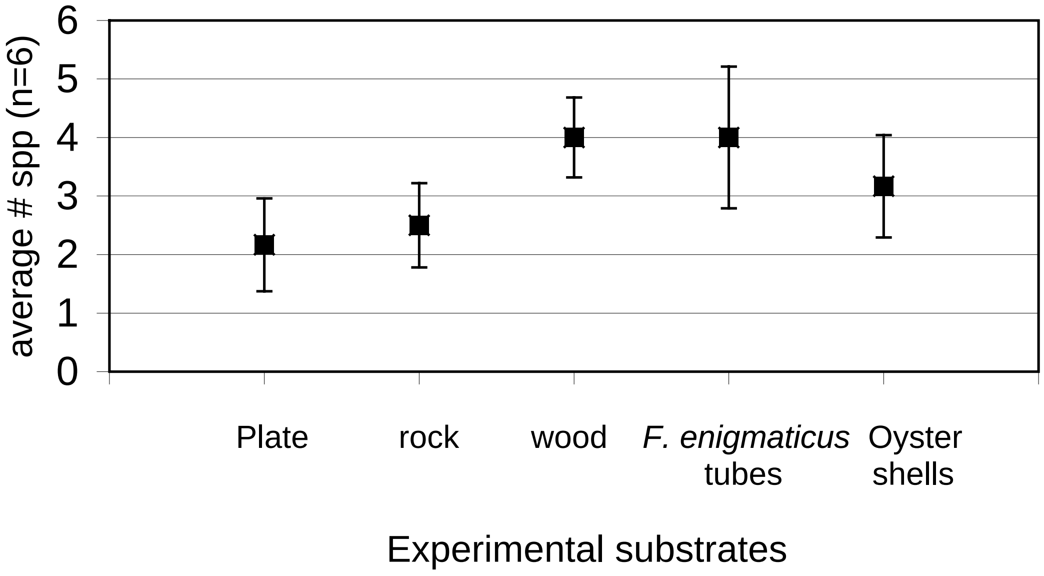


Fig. 1.4 The number of species recruiting to each experimental substrate type averaged across the six sites. Error bars are standard error.



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-CHAPTER TWO-

Fouling community development throughout a highly invaded and anthropogenically modified central Californian estuary

ABSTRACT

Estuaries, which are historically dominated by soft sediment communities, face anthropogenic modifications that enhance the quantity of hard structures and the diversity of species that can utilize this once limited substrate. To understand what factors control the development of communities on hard substrates and how these factors vary throughout an entire system, recruitment plates were deployed at ten sites within the central Californian estuary Elkhorn Slough. The influence of environmental variables, species life history traits, and timing of plate deployment were examined through a 2.5 year study. Location within Elkhorn Slough had the greatest influence over the development of assemblages; each site's assemblage differed significantly in species identity and abundance from all other sites suggesting that differing local abiotic and biotic processes influence assemblage development. Recruitment limitation influenced assemblage development throughout the system, as indicated by poor recruitment of long-lived bivalve species and consistent availability of free space on experimental plates even after 2.5 years in the field. Environmental conditions, such as variable salinity, may underlie the dominance of low salinity tolerant species such as the polychaete *Ficopomatus enigmaticus* and the barnacle *Balanus glandula* at some sites. Some assemblage development patterns are attributed to possible competitive interactions between fouling species, most notably between the non-native bryozoans *Amathia vidovici* and *Bugula neritina*. However, biotic interactions play an important assemblage-structuring role at only two sites. Recruitment limitation, salinity fluctuations, and competitive interactions between ephemeral species are important processes that controlling the development of assemblages within Elkhorn Slough; however, the most important processes influencing assemblage development differ

between locations. Extrapolating patterns and processes of assemblage development from one location in Elkhorn Slough to another may rarely be appropriate.

INTRODUCTION

An estuaries is broadly defined as the portion of earth's coastal zone where salt and fresh water interact (Day et al. 1989). Many of the largest estuaries are found at the mouths of great rivers or in the low-relief coastal plains of Europe and the east coast of North America (Day et al. 1989). Estuaries are composed of a variety of environments from high-energy beaches to wetlands and oligohaline transitional zones between fresh and salt water. Most of these environments are depositional habitats characterized by muddy and sandy substrates supporting primary producers such as marsh plants, sea grasses, and benthic algae (McLusky and Elliott 2004). While some of these environments have low species diversity, most are highly productive and support abundant transient species, such as migrating fish and shore birds, and resident consumers, such as bivalves and crustaceans. In many coastal ecosystems (for example rocky shores, coral reefs, and kelp forests) complex structural habitats are common and a large portion of the biodiversity is composed of species that are adapted to attach to hard substrates (fouling species). In estuaries the majority of species are adapted to live in soft sediments. Even the oysters and mussels, which may rely on hard attachment sites, are capable of attaching to the shells of conspecifics, negating the need for other hard substrates.

Estuaries are frequently centers for major urban development because of their sheltered access to coastal environments. As such, many estuaries face multiple human disturbances which alter habitats, water quality and hydrology, and change the structure of biological communities (Day et al. 1989). Many estuaries and embayments throughout the world have been developed into major harbors to support international shipping (Hedgpeth 1979; Day et al. 1989; McLusky and Elliott 2004). This development results in extensive habitat modification including dredging and other alterations to hydrology, as well as the addition of structures such as seawalls, bridges, and floating docks (Day et al. 1989). Anthropogenic structures offer new ubiquitous habitats for the development of fouling communities, historically uncommon assemblages in estuaries (Chapman and Bulleri 2003). As a widely distributed and increasingly abundant community type, it is important to understand the processes structuring these assemblages (Connell and Glasby 1999).

Anthropogenic substrates have repeatedly been shown to support assemblages that differ from those occurring on nearby natural rocky environments (Connell and Glasby 1999; Glasby and Connell 1999; Connell 2000; Chapman and Bulleri 2003). These communities are frequently dominated by non-native species (Ricketts et al. 1985; Wasson et al. 2005). Many non-native species have broad environmental tolerances and are able to establish in a wide range of environmental conditions (Carlton 1979). Additionally, many non-native species are able to rapidly utilize resources when they become available allowing them to quickly colonize new open space (Rejmanek and Richardson 1996). As the abundance of artificial structures in estuaries increases, it is likely that non-native species will rapidly colonize these habitats.

Given the increasingly urbanized habitats in estuaries and the dominance of non-native species in these environments, can the principles of ecological succession be applied to understand how highly invaded fouling estuarine communities develop on anthropogenic structures? Ecological succession was defined historically as the orderly process of community development that is directional and predictable, resulting from modification of the physical environment by members of the community, and culminating in a stable community in which maximum biomass or high informational content is maintained (Odum 1969). More modern definitions omit the directional and predictable requirements and the “stable” community outcome to define succession as the sequence of changes in community structure occurring after a site has been disturbed (Connell and Slatyer 1977; Farrell 1991; Berlow 1997). Noting that succession is inherently a historical process, much research has focused on identifying past events which explain observed variation in community structure (Clements 1916; Sousa 1979; Farrell 1991; Berlow 1997; Benedetti-Cecchi 2000; Kocak and Kucuksezgin 2000). Events influencing community development can be grouped into two broad categories: 1) external physical and biological events such as disturbances, changes in environmental conditions, and recruitment/dispersal events, and 2) local biological interactions such as competition, predation, and facilitation among species at different successional stages.

Which of the two event types is more important to community development determines which of the following three succession patterns occur. In situations where biological interactions are most important, early species have strong and consistent effects on later species resulting in communities that develop along predictable pathways that change over time, or *canalized succession* (Odum 1969; Connell and Slatyer 1977; Farrell 1991; Berlow 1997). In canalized succession, community composition is largely determined by the length of time since the last disturbance event (Berlow 1997). If physical events are more important than species interactions, variation in developing community structure may be driven by "external" events such as environmental conditions, propagule availability, and disturbance regimes, resulting in *externally driven succession* (Sousa 1979; Gaines and Roughgarden 1985; Berlow 1997). In externally driven succession, variation in community composition is best explained by a combination of site characteristics not species interactions (Berlow 1997). In other situations, the strength of species interactions is determined by context and resulting successional patterns are highly contingent and rarely repeatable, known as *contingent succession* (Oshurkov 1992; Berlow 1997). In these cases, detailed knowledge of species interactions and how these interactions vary in space and time is needed to understand resulting community structure (Berlow 1997).

Canalized fouling community succession follows a series of generalized stages described by Scheer (1945): (1) the development of a biofilm; (2) the colonization by short-lived rapidly-growing (ephemeral) algae or colonial species such as bryozoans and tunicates; (3) the replacement of these ephemeral assemblages by a persistent "climax" community, dominated by slow-growing, longer-lived bivalves such as oysters and mussels. This pattern of canalized fouling community succession has been observed by many subsequent researchers (Dean and Hurd 1980; Chalmer 1982; Rajagopal et al. 1997; Lin and Shao 2002; Berntsson and Jonsson 2003). When deviations from this scheme of fouling community development were observed, authors invoked a number of external mechanisms that prevented the orderly and predictable replacement of one set of organisms by another: inconsistent larval supply and seasonality of species growth and recruitment (Chalmer 1982; Brown and Swearingen 1998; Watson and Barnes 2004), stressful environmental conditions with frequent disturbances (Osman 1977), and biotic characteristics of the organisms themselves such as their short life spans (Sutherland and Karlson 1977).

The central Californian estuary Elkhorn Slough affords the opportunity to study the development of fouling communities throughout a system, which has rarely been done (but see Kocak and Kucuksezgin 2000; Watson and Barnes 2004; Brown and Swearingen 1998). Elkhorn Slough has undergone extensive hydrological manipulations including the creation of a stable opening to the ocean, the construction of a harbor, and the diking of much of its wetlands for cattle farming (Van Dyke and Wasson 2005). At only 11 km in length, Elkhorn Slough is small enough for one to gain an understanding of fouling community development on a system-wide level, yet due to human modifications it contains a variety of environmental regimes such that different succession processes may control community development at different locations. Prior research in Elkhorn Slough has shown that fouling communities are predominantly composed of non-native species (Wasson et al. 2005). Many of these non-natives have broad environmental tolerances and life history traits (frequent spawning and long larval pelagic phases) that may promote rapid colonization of free space. Interactions between native and non-native fouling species and/or different external events may direct fouling assemblage development. Through the deployment and multi-year monitoring of a series of recruitment plates, I explored the development of fouling assemblages under differing environmental regimes to determine how succession occurs throughout this highly invaded and anthropogenically modified estuary. Specific attention was given to the role of species life history characteristics and interactions as well as environmental parameters and events in assemblage development.

METHODS

Recruitment plates

Ten recruitment stations were set up, spanning the length of Elkhorn Slough and encompassing a variety of distinct environmental settings (Fig. 2.1). All of the stations were established at 0 m MLLW ± 0.2 m on mudflats. At each station, 6 or

12 replicate recruitment plates made of PVC rectangles (5 cm x 10 cm), coated with 3M™ Safely-Walk™ no-skid traction adhesive were deployed randomly and equally between two PVC racks (Fig. 2.1). Prior to development, plates were bathed in flowing filtered seawater for one week, to allow chemical contaminants from the PVC and no-skid to diffuse into the seawater. A bolt through the center attached each plate to the PVC racks such that all plates were oriented perpendicular to the water's surface and their bottom edge was 15 cm above the substrate (Fig. 2.1b). This orientation was chosen to mimic the orientation of pilings, the most common and widespread human added hard substrate in Elkhorn Slough (Chapter 1).

Six recruitment plates were deployed, three per rack, in May 2002 (at six sites) and another six plates in August 2002 (at ten sites), to address how temporal variability in larval recruitment influences the development of fouling communities. Plates were retrieved from the intertidal racks during low tides, digitally photographed, and returned to the racks once a month until October 2004. The total length of time in the field for the May 2002 and August 2002 deployments were 30 months and 27 months respectively. Species on each plate were either identified in the field, or when needed, samples were collected and identified under dissecting microscopes in the lab. Percent cover of each species was quantified from digital photographs of each plate's back and front using the image-analysis software, ImageJ©. On October 25th 2004, plates were recovered from the field, photographed one final time, then brought back to the lab. Working with Smithsonian Estuarine Research Center Taxonomists (C. Brown and C. Zabean), all organisms attached to the plates, including cryptic species that may not have been identified from the digital photographs, were identified to the lowest taxonomic level possible. Photographs provide time-series data on recruitment, survivorship, growth, and development of fouling communities at different locations and under varying environmental conditions in Elkhorn Slough. The average monthly percent cover was calculated for each site by deployment date for subsequent analysis.

Summary of analyses

To explore the influence of timing of substrate availability, surrounding communities, and environmental parameters on plate assemblage development, the following data were collected and analyses performed. 1) The influence of timing of substrate availability on fouling assemblage development was addressed by comparing assemblage structure from the two different deployment dates, shortly after the second deployment and at the end of the experiment. 2) To identify whether assemblages on plates were similar to fouling communities in the surrounding environment, surveys of all fouling species within 20 m of experimental recruitment racks were conducted. The assemblages on the plates and in the local environment were compared with multivariate statistics. 3) Biotic interactions frequently structure communities. To explore whether biotic interactions, such as competition, influence the development of plate assemblages, I graphed monthly species percent cover by site and conducted statistical analyses on species pairs with oscillating offset abundances, a possible indication of competition. 4) Finally, I sought evidence of Scheer's (1945) fouling community successional pathway by tabulating recruitment/regrowth frequency of ephemeral and persistent species over time. If Scheer's successional pattern is occurring in plate assemblages, than there would be reduced ephemeral species recruitment and increased persistent species establishment with time. 5) Environmental parameters influence where species can establish and persist. To understand if there were differences between the physical environment at each recruitment site, I measured salinity, temperature, flow speed, and suspended particulate matter in the water column at all recruitment sites. Sites were grouped statistically (PCA) by their environmental parameters, then this grouping was compared to site ordinations based on recruitment assemblage structure (nMDS).

Surveys of surrounding communities

Because developing plate assemblages may reflect recruitment from local sources, I surveyed all fouling communities within 20 m of each set of recruitment plates in June 2003 and December 2003. By carefully examining all hard substrates within 20 m of the racks, I developed species lists for each site. The surveys were limited to organisms attached to hard substrate and greater than 0.5 cm in maximal diameter, the resolution observable from the digital pictures of the recruitment plates. Species that could not be identified in the field were brought back to the lab for identification under dissecting microscopes.

Environmental monitoring

Temperature was recorded every 30 minutes with iButton® temperature loggers taped to one rack at each site and replaced monthly. Salinity of the water directly adjacent to the recruitment plates was measured every month with a handheld refractometer. Flow at each site was measured simultaneously on three separate ebb or flood spring tides (7/1/2003, 1/19/2004, 9/14/2004). To do this, ten people were distributed among the ten recruitment sites. Each person stood between the two recruitment racks and timed how long it took for a neutrally buoyant piece of paper to travel 1 m. Measurements were repeated there times every ten minutes for two hours during rapid tidal exchange events. Simultaneous measurement allowed flow rates between different locations within Elkhorn Slough to be compared. Prior to flow measurement, each person collected one liter of water from the site, being careful not to disturb underlying sediments. The water samples were drained through pre-weighted 20 μm filter paper and dried at 60°C for two days. The paper and associated sediment were then weighed and the initial weight subtracted to calculate the amount of suspended particulate material in the water column of each site. I gathered three additional water samples from each site, during photographic monitoring, for a total of six suspended particulate measurements. The mean and coefficient of variance were calculated for each sites environmental variables.

Statistics

To determine if there was a difference in assemblage structure between different deployment dates, the average monthly species percent cover by deployment date was compared from the six sites with both May and August deployments. nMDS ordinations based on Bray-Curtis similarities from square-root transformed average percent cover data were calculated to graphically display the similarity between assemblages from different sites and different deployment dates (Clarke and Warwick 1994). Two 1-way analyses of similarity (ANOSIM) were calculated on the Bray-Curtis square-root transformed assemblage data to determine if deployment date or site explained more of the observed variance in assemblage structure (Clarke and Warwick 1994). Similarity percentage (SIMPER) was calculated to determine which differences in species percent cover were responsible for the observed dissimilarity between assemblages (Clarke and Warwick 1994). To understand if date of deployment mattered in early assemblage development and/or later development, two sampling dates (December 2002 and October 2004) were compared as described above.

To determine if species recruiting to the plates were similar to species found in the local environment, species lists from surrounding fouling community surveys were compared to species attached to the experimental fouling plates from the same month as the surveys (July 2003 and December 2003). Percent cover of species on plates was transformed into presence/absence species lists and nMDS plot was created from a Bray-Curtis similarity matrix of the survey and plate assemblages (Clarke and Warwick 1994). Two 1-way ANOSIM tests were conducted to determine if species in the local environment differed from assemblages developing on recruitment plates or if variation in assemblage composition was explained by site (i.e. location within Elkhorn Slough) (Clarke and Warwick 1994). SIMPER was conducted to determine which species drive significant observed assemblage differences (Clarke and Warwick 1994).

To explore the role of species identity and interspecific interactions in community development, I examined individual species colonization and growth patterns. Species' average monthly abundances were graphed by site and deployment date. *Amathia vidovici* and *Bugula neritina* were observed to increase in abundance as the other decreased in abundance. To determine if there was a relationship between the changes in these two species' percent cover, I ran a cross correlation on the time series of average percent cover by month for each site with the two species. I used only the August deployment dates because this deployment occurred at all sites.

To understand the role of non-native species in fouling community development all species observed on recruitment plates or in the local environment were categorized as native or non-native to Elkhorn Slough based on the following references (Carlton 1979; Ruiz et al. 2000; Wasson et al. 2001; Wasson et al. 2005).

To evaluate whether Scheer's (1945) canalized successional pathway occurs in Elkhorn Slough fouling communities, species were categorized as ephemeral or persistent, based on their average duration on experimental fouling plates across all sites. Ephemeral species were categorized as species with individuals or colonies that occupied space on fouling plates for less than 12 consecutive months. Persistent species' colonies or individuals occupied plate space for over 12 consecutive months. To understand if persistent species recruited more frequently after ephemeral species established, two analyses were conducted. First, the order of species arrival was tabulated. Then the average, range, and standard deviation of species arrival order across all sites were calculated. Second, the 27-30 month time series of average species percent cover by site and deployment date was divided into four periods, roughly seven months long each: (1) deployment - December 2002, (2) January 2003 - July 2003, (3) August 2003 - February 2004, (4) March 2004 - September 2004. The final date (October 2004) was omitted from this analysis because it contains data from the careful lab search for cryptic species and is not directly comparable to the photographic sampling procedure used to identify and quantify assemblages on all prior dates. The number of times a large-scale recruitment or re-growth event (defined as a doubling or more in percent cover across all plates at a site) occurred for persistent and ephemeral species was tallied for each time period. A 2 x 4 contingency table was calculated to identify if patterns in the timing of ephemeral and persistent species recruitment followed Scheer's (1945) canalized fouling community succession, with ephemeral species recruiting initially followed by enhanced persistent species recruitment with time.

To determine if and which environmental variables influence recruitment and fouling assemblage development, I conducted a Principal Component Analysis (PCA) for the ten recruitment sites using the measured environmental variables (means and coefficients of variance) to characterize the sites. The PCA provided insight into which environmental variables differed between sites and which sites were more similar based on the measured environmental parameters. To match environmental patterns with observed biotic patterns on recruitment plates, I used BIO-ENV within the PRIMER V5 software (PRIMER-E Ltd, Plymouth, UK). In BIO-ENV, a similarity matrix based on Euclidean distance was created for the environmental parameters and was compared via Spearman rank correlation to the Bray-Curtis similarity matrix for average percent cover on plates from October 2004. The BIO-ENV identifies the combination of environmental variables that groups the sites in a manner most consistent with the biotic patterns (Clarke and Warwick 1994). RELATE, a permutation test in the PRIMER V5 software (PRIMER-E Ltd, Plymouth, UK), was then used to identify whether the above BIO-ENV test had statistically significant results (i.e. if the environmental and biotic similarity matrices had similar among-sample rank similarities) (Clarke and Warwick 1994). Environmental variables that could explain differences between sites were graphically overlaid on the nMDS plot of the average percent cover of recruited species from October 2004.

RESULTS

A total of 28 species or species complexes from nine phyla recruited to experimental plates across the ten study sites (Table 2.1). Some of the most common species recruiting and establishing on the experimental plates included the native barnacle *Balanus gladula* and the non-native erect bryozoans *Bugula neritina* and *Amathia vidovici* (Table 2.1). Over half of the sites had diverse fouling assemblages with ten or more species or species complexes establishing on the plates over the 27-30 months of the study (sites B, C, D, E, F, and I). The remaining sites had less diverse assemblages ranging from eight (site J) to as little as two species (site G) (Table 2.1). Average percent cover of non-natives on plates at the end of the deployment ranged from 83.6% (site I) to 0% (site G). By the end of the experiment, non-natives covered more surface area than natives at six sites (sites A, B, C, E, I, and J). At the other four sites native species occupied more surface area than non-natives by October 2004 (sites D, F, G, and H).

The timing of substrate availability (deployment date) did not influence early or final assemblage structure. Comparing plate assemblages from the two deployments in December 2002 (after 4 or 7 months in the field) showed that deployment date did not explain differences in assemblage structure but site did (1-way ANOSIM deployment date: Global *R* = -0.102, *p* = 0.85; 1-way ANOSIM site: Global *R* = 0.672, *p* = 0.001) (Fig. 2.2). Most of the species establishment observed during this initial period occurred in the fall after the August plates were deployed. Twelve of the 16 species recruitment events observed during this period occurred between September 2002 and November 2002, after the second set of recruitment plates had been deployed. Thus, larvae from the same recruitment events colonized plates from both deployments. Half of the sites were characterized by one abundant species, which was not abundant at other sites. Site B had *Ficopomatus enigmaticus*, site C had *B. neritina*, and site G had *B. glandula* (Fig 2.3). Site A had almost no recruitment, and sites D and E had sparse but diverse recruitment, with 5 and 4 different species recruiting respectively, but in low abundances (Fig 2.3). Dominant species differences explained most of the early between-site assemblage variation.

Comparing plate assemblages from the final date, October 2004, after 27-30 months in the field, supported earlier findings. Deployment date did not affect final assemblage composition whereas site continued to explain a large portion of the observed variation in different assemblage structure (1-way ANOSIM, deployment date: Global *R* = -0.141, *p* = 0.89; 1-way ANOSIM, site: Global *R* = 1.00, *p* = 0.001) (Fig. 2.2). Most of the sites remained characterized by one or two abundant species. While some species were abundant at more than one site, the same combination of abundant species was not observed at multiple sites. For example, 24.6% of the available surface area at site A was occupied by *F. enigmaticus*. Site B's plates were occupied by *B. glandula* (24.2%), *Haliclona/Halichondria* complex (16.5%), and *F. enigmaticus* (22.5%) (Fig. 2.3); whereas plates at site G were almost exclusively colonized by *B. glandula* (Fig 2.3). The differences in dominant species explained observed assemblage differences between sites at both initial and final sampling periods.

Plate assemblages were different from fouling assemblages on nearby hard substrates in the summer but not in the winter. When assemblages on plates were compared to fouling species found within 20 m of the plates, significant differences were observed in July 2003 (ANOSIM, env vs. plate: Global *R* = 0.565, *p* = 0.001) and nearly significant differences in December 2003 (ANOSIM, env vs. plate: Global *R* = 0.108, *p* = 0.069) (Fig. 2.4). *B. glandula* and *B. neritina* were more common on the plates than in the surrounding environment whereas *F. enigmaticus* and *Haliclona/Halichondria* complex were more common in the surrounding environment (together accounting for nearly 30% of the observed differences between plates' and sites' assemblages). There was a significant site difference in July 2003 (ANOSIM, site: Global *R* = 0.184, *p* = 0.048) and December 2003 (ANOSIM, site: Global *R* = 0.502, *p* = 0.001) with each site dominated by a distinct set of species (Fig 2.3).

There are indications that species interactions, such as competition, structured some of the plate assemblages. Species replacement, or change in the identity of the dominant species, was observed at five out of the ten sites (sites B, C, F, I, J) (Fig. 2.3). At the other five sites, whichever species initially colonized the plates persisted as the dominant space-occupier throughout the course of the study. The switch in dominance commonly occurred between *Amathia vidovici* and *B. neritina* (sites C, I, J) or between different *Ulva* species (site F). Site B had three different dominant species (each occupying more than 30% of the surface area of site B's plates), starting with *B. glandula,* then *B. neritina,* and finally *F. enigmaticus*. Cross correlation analysis of the time series of abundance of *A. vidovici* and *B. neritina* illustrates different patterns at the four sites with both species (sites C and J have 3 peaks and troughs and sites B and I have four (Fig. 2.5)). A significant positive cross correlation occurred at negative eleven months lag at site C, meaning that when one species was abundant, eleven month later the other species was abundant. A significant negative cross correlation occurred at lag zero for Site J, indicating that when one species was abundant the other species was not abundant (Fig. 2.5). Site B had a significant positive correlation at lag zero and site I at negative four months. The lack of a consistent pattern between the four sites, both in correlation timing and number of peaks and troughs, implies that seasonality is not consistently responsible for the changing dominance patterns. Rather some direct or indirect biotic interaction, possibly site specific, is responsible for observed dominance switching (Fig. 2.5).

There is little evidence that Scheer's (1945) successional pathway occurred on plate assemblages in this system. Scheer's (1945) "climax" fouling community bivalve species, i. e. oysters and mussels, did not dominate any of the fouling plate assemblages at any time during the experiment, even though bay mussels and *Ostrea conchaphila* recruited in low abundances to 5 sites (Table 2.1) and were found throughout the system (Chapter 1, Fig. 1.2). The other persistent species in this study, *F. enigmaticus*, and *Balanus glandula* however, did increase in abundance over time and came to dominate some sites. In contrast to Scheer's proposal, the five persistent species in this study established early, for example *B. glandula* ranged from the first to the fifth species to establish at a site (Table 2.1). Over half of the ephemeral species recruited, on average, after all five of the persistent species. The tabulation of ephemeral and persistent species recruitment events across the four time periods indicates fewer than expected persistent species and greater ephemeral species recruitment events in the last seven months of the study as compared to the rest of the study (chi-squared = 15.3, df = 3, *p* = 0.002). This finding does not support Scheer's (1945) hypothesis of persistent species increasing over time and replacing ephemeral species. Additionally, the second time period from January 2003 –July 2003 experienced more persistent species and less ephemeral species recruitment than expected.

Some plate assemblage differences were explained by between site environmental variability. Between site differences in mean flow and temperature as well as salinity variability explained 68% of the variation in plate assemblage structure. A PCA of sites based on the mean and coefficient of variation (CV) for each measured environmental variable (salinity, flow, temperature, and suspended particulates (Table 2.2)) had a primary principle component axis (PC1) explaining 41.8% of the variation and comprised primarily of flow and temperature (mean flow eigenvector = 0.434, mean temperature eigenvector = -0.358) and a secondary principle component (PC2) axis explaining 18.9% of the variation and comprised primarily of variation in suspended particulates and salinity (suspended particulates CV eigenvector = -0.588, Salinity CV eigenvector = 0.390). Five sites (A, B, C, E, and J) cluster into a group with negative PC1 and positive PC2 values (Fig. 2.6e). Sites I and D group near the zero value for PC1, with G and F far offset from the other sites with high PC1 values. Sites G and F are near the mouth of Elkhorn Slough and have flow rates almost twice as high as any of the other sites (Fig 2.6b). When an nMDS ordination based on Bray-

Curtis similarities in biotic data from October 2004 was conducted, the distribution of sites was similar to the PCA with B, C, and J remaining clustered and F and G set apart form the other sites (Fig. 2.6a, e). BIO-ENV found the combination of mean flow, salinity CV, and temperature mean and CV resulted in a 0.682 correlation between the biotic and environmental similarity matrices. The above correlation was shown to be statistically significant through RELATE with a Rho = 0.439 and $p = 0.026$.

DISCUSSION

Fouling assemblage development was highly dependent on location within Elkhorn Slough and not on timing of deployment or adjacent communities. Different processes seemed to be responsible for guiding succession at different locations. In sites with highly variable salinity, external forcing may limit colonization of recruitment plates to low salinity tolerant species. Under less variable environmental conditions, there is evidence that species interactions play an important role in assemblage development. However, the species interactions observed in this system usually cause an oscillation in dominance among ephemeral species, not the replacement of ephemeral species by longer-lived persistent species. There is little evidence at any of these sites of Scheer's canalized successional pathway of fouling community development (1945). This is due, at least in part, to limited recruitment of persistent bivalves (i.e. oysters and mussels), which comprise Scheer's final successional stage (Scheer 1945).

Unlike the many previous fouling community studies (Osman 1977; Sutherland and Karlson 1977; Brown and Swearingen 1998; Lin and Shao 2002; Watson and Barnes 2004), the timing of settlement plate deployment did not make a difference to early or later assemblage structure. Very few species and individuals recruited to the May settlement plates before the August plates were deployed. As a matter of fact, sites A, B and E experienced no recruitment during these months and only site C experienced recruitment in August just prior to the second plate deployment. Most of the recruitment occurred after the second set of recruitment plates was available for colonization, exposing both sets of plates to the same propagule pool.

The strikingly low recruitment from May to August 2002 in this central Californian estuary could be due to failed spawning, larval death, larval displacement or advection out of the system, or selective larval settlement elsewhere. Offshore events in California upwelling regions, such as entrapment in currents and predation on larvae, have been shown to contribute to rocky shore recruitment limitation (Roughgarden et al. 1988). It is possible that similar events may limit estuarine larval availability. Elkhorn Slough also has some of the highest nitrate concentrations measured in any estuary. Measurements near site G average 1,000 μm and sometimes exceed 5,000 μm (Caffrey 2002). These high nitrate levels are attributed to the use of fertilizers on nearby agricultural fields (Caffrey 2002) and may be lethal to benthic organisms and larvae (Tilak et al. 2002). Elkhorn Slough is also the site of a Duke power plant that draws water from the slough for coolant purposes (Silberstein et al. 2002). In the process, a portion of the larvae in the water used for coolant are killed, possibly decreasing the total number of larvae that can colonize available substrates (Foster 2005). Low recruitment to newly available substrate may also be due to selective settling of larvae. Many fouling organisms, such as *Ficopomatus enigmaticus* and *Ostrea conchaphila* are gregarious settlers (Couch and Hassler 1989; Toonen and Pawlik 1994). Their larvae actively seek adult populations and attach on or near conspecifics. The gregarious settlement behavior of *F. enigmaticus* is most likely the reason why this non-native tubeworm took nearly a year to colonize recruitment plates at site A, located 20 m from a large adult population. The system-wide recruitment limitation is an external event that strongly structures fouling community development throughout Elkhorn Slough.

Most of the observed patterns of assemblage development appear to be controlled by external events such as recruitment limitation and stressful environmental conditions such as fluctuating salinity (externally driven succession). As discussed above, recruitment limitation was evident across a number of sites during the initial months of study. Recruitment continued to be limited at many sites throughout the study, as evidenced by the large amount of unoccupied space on experimental plates at sites A, D, E, H, and J throughout the study. There was not enough recruitment at these sites to create assemblages that fully utilized provided hard substrate resources. When resources are not limited, competitive species interactions do not play an important role in structuring communities (Valiela 1995). The other possible explanation for the persistent availability of unoccupied space is low growth rates. However, this was not observed in the field. Organisms that recruited to plates grew rapidly (personal observations).

Stressful environmental conditions may also structure communities at some Elkhorn Slough locations. Sites A and G, the two sites with the greatest salinity fluctuation, have low diversity assemblages dominated by a single low salinity tolerant species (Hill 1967; Dineen and Hines 1994; Anil et al. 1995). Site A is dominated by *F. enigmaticus* and site G by *Balanus glandula*. Seasonal growth and recruitment patterns also shape assemblage development at some locations. Seasonal growth and senescence of ephemeral algae occurred at site F. The ephemeral bryozoan, *Bugula neritina* appears to recruit in fall, grow throughout winter, and die back in spring at the tidally exposed sites B, C, and E.

There is some evidence that species interactions structure assemblage development but only at some locations within Elkhorn Slough (contingent succession). *Amathia vidovici* and *Bugula neritina* may compete with one another, resulting in alternating dominance patterns most clearly visible at the two lagoon sites, I and J. Bryozoan species are known to compete in other fouling environments. For example, on Alaskan intertidal and shallow subtidal rocks interspecific competition between bryozoans frequently results in either the complete overgrowth of a competitively inferior species by a competitively superior species or the mutual overgrowth of competitively comparable species (Barnes and Dick 2000). Unlike Scheer's canalized sequence of fouling community development, none of the observed interactions led to early-arriving ephemeral species replaced by late-arriving persistent species (Scheer 1945). Rather, when species interactions appeared to drive assemblage development patterns, the resulting community oscillated between different ephemeral species. In canalized succession, time from disturbance predicts whether ephemeral or persistent assemblages dominate the community (Berlow 1997). However, in Elkhorn Slough fouling communities time since deployment does not predict which of the several ephemeral communities occurs. Additionally, the five persistent species were early settlers at many locations. *B. glandula* was one of the first colonizers at sites C, E, G, and H, and *F. enigmaticus* was the first to colonize sites A and B. This implies that these species do not rely on ephemeral species to modify the substrate or habitat before they could colonize, a common feature of canalized succession (Connell and Slatyer 1977; Berlow 1997). However, there is some indication that certain ephemeral species may rely on habitat modification before colonization. *Diadumene lineata*, *Watersipora subtorquata*, and *Bowerbankia gracilis* occurred at multiple sites but not until many other species established, indicating possible facilitation between established assemblages and these colonizing ephemerals.

Location within Elkhorn Slough appears to be the most important driver of fouling assemblage development. Some of the effects of location on assemblage structure and developmental processes can be attributed to variation in measured environmental parameters between sites, such as freshwater input, flow rates, and temperature. Recruitment limitation, an important assemblage-structuring factor, also appeared to vary by location. Characteristics of some sites, such as tidal restriction in lagoons, may increase recruitment by trapping locally produced larvae and preventing larval advection. However, none of the assemblages at a given location within Elkhorn Slough are identical. Initially developing plate assemblages are not similar to assemblages growing on hard substrates in the local environment. Overtime, however, plate assemblages do begin to converge with nearby fouling communities. The lack of similarity between plates and fouling communities at the sites may be due insufficient time for assemblage development, this is especially likely given the high levels of recruitment limitation within Elkhorn Slough. Another possible explanation is variation in substrate type. The plate assemblages developed on PVC whereas fouling communities at sites where growing on any number of substrates, including wood, concrete, peat, rocks, and shell fragments (personal observations). At locations with greater resource utilization (less free space availability) competitive species interactions may have played a role in structuring communities. With the dramatic differences in both plate assemblage structure and developmental processes, observations from one site's recruitment plates could not necessarily be extrapolated to other locations throughout the system. Elkhorn Slough demonstrates how variable community developmental patterns can be, even within a well defined system only 11 km in length.

Caution must be taken when focusing on one or a few study locations and extrapolating to larger system processes.

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Table 2.1 List of organisms established on recruitment plates (species complexes were used when visual identification from photographs was not reliable enough for more detailed classification). Order of species recruitment at each experimental site listed numerically under the site heading. Bold species are non-native. E = ephemeral. P = persistent.

		Ephemeral/					Site								
Species	Phylum	Persistent	A	B	C	D	E	F	G	H	I	J	Avg	SD	Range
Filamentous red	Rhodophyta	E						1			1		1	0.0	1
Botrylloides sp.	Chordata	E					2						2	n/a	2
Bugula neritina	Bryozoa	E		6	1	3	2				2	1	2.5	1.9	1--6
Conopeum osburni	Bryozoa	E	2	2	2	3	2				4		2.5	0.8	2--4
Balanus gladula	Crustacea	P	3	3	1	2	1	4	2	1	5	4	2.6	1.4	1--5
Ficopomatus enigmaticus	Annelida	P	1	1	6	7	4						3.8	2.8	1--7
Ulva linza	Chlorophyta	E			11	1	5	2					4.75	4.5	1--11
Caulacanthus ustulatus	Rhodophyta	E			5								5	n/a	5
Ulva fenestrata	Chlorophyta	E				7		3					5	2.8	3--7
Bay mussel complex	Mollusca	P			5								5	n/a	5
Ostrea conchaphila	Mollusca	P	4	5	7	4	5						5	1.2	4--7
Balanus improvisus	Crustacea	P		5	6	6		7	1				5	2.3	1--7
Haliclona /Halichondria spp.	Porifera	E	6	2	8	11	5				2	2	5.14	3.5	2--11
Diadumene lineata	Cnidaria	E		6			7			2	8	5	5.6	2.3	2--8
Chthalamus sp.	Crustacea	E				9		5		3			5.67	3.1	3--9
Watersipora subtorquata	Bryozoa	E		9	3	11	3	8			3	3	5.71	3.5	3--11
Cryptosula pallasiana	Bryozoa	E		8	4	5	3	12			4		6	3.4	3--12
Ectopleura crocea	Cnidaria	E		7	10						1		6	4.6	1--10
Ulva intertinalis	Chlorophyta	E		4		10		6					6.67	3.1	4--6
Amathia vidovici	Bryozoa	E		7	8	11	5				7	2	6.67	3.0	2--11
Schizoporella unicornis	Bryozoa	E						9			6		7.5	2.1	6--9
Bowerbankia gracilis	Bryozoa	E	5	9	9	11	6	11			7	5	7.88	2.5	5--11
Gracilaria sp.	Rhodophyta	E				8							8	n/a	8
Bugula stolonifera	Bryozoa	E									10	6	8	2.8	6--10
Diadumene leucolena	Cnidaria	E									9		9	n/a	9
Obelia sp.	Cnidaria	E						10					10	n/a	10
Diadumene franciscana	Cnidaria	E									11		11	n/a	11
Spirorbids	Annelida	E				12							12	n/a	12
		TOTAL SPECIES	**6**	**14**	**15**	**17**	**13**	**12**	**2**	**3**	**15**	**8**			

Table 2.2 Environmental variables at each recruitment site. Mean (coefficient of variance).

Site	Flow m/s (n=80~100)	Suspended particulates g/l (n=6)	Salinity ppt (n=26, 29)	Temperature °C (n=~4500)	Distance from mouth km
A	0.040 (0.492)	0.205 (0.471)	32.39 (0.29)	17.760 (0.249)	9.943
B	0.045 (0.694)	0.277 (0.518)	36.17 (0.08)	17.219 (0.239)	8.182
C	0.076 (0.953)	0.246 (0.470)	35.97 (0.09)	17.293 (0.213)	7.104
D	0.075 (0.603)	0.232 (0.598)	36.34 (0.06)	16.339 (0.222)	4.921
E	0.026 (0.944)	0.236 (0.429)	36.07 (0.06)	16.078 (0.228)	5.318
F	0.139 (0.792)	0.207 (0.565)	35.64 (0.06)	14.207 (0.158)	0.435
G	0.140 (0.601)	0.221 (0.519)	15.41 (0.45)	15.318 (0.183)	2.335
H	0.079 (0.992)	0.255 (0.606)	38.00 (0.10)	18.201 (0.333)	8.267
I	0.075 (0.992)	0.208 (0.565)	38.58 (0.09)	17.448 (0.231)	6.648
J	0.009 (1.089)	0.274 (0.487)	36.65 (0.07)	17.784 (0.233)	5.924

Fig. 2.1 a) Location of recruitment sites. Letters on the map correspond to site labels. b) Graphic depiction of recruitment plate deployment on racks.

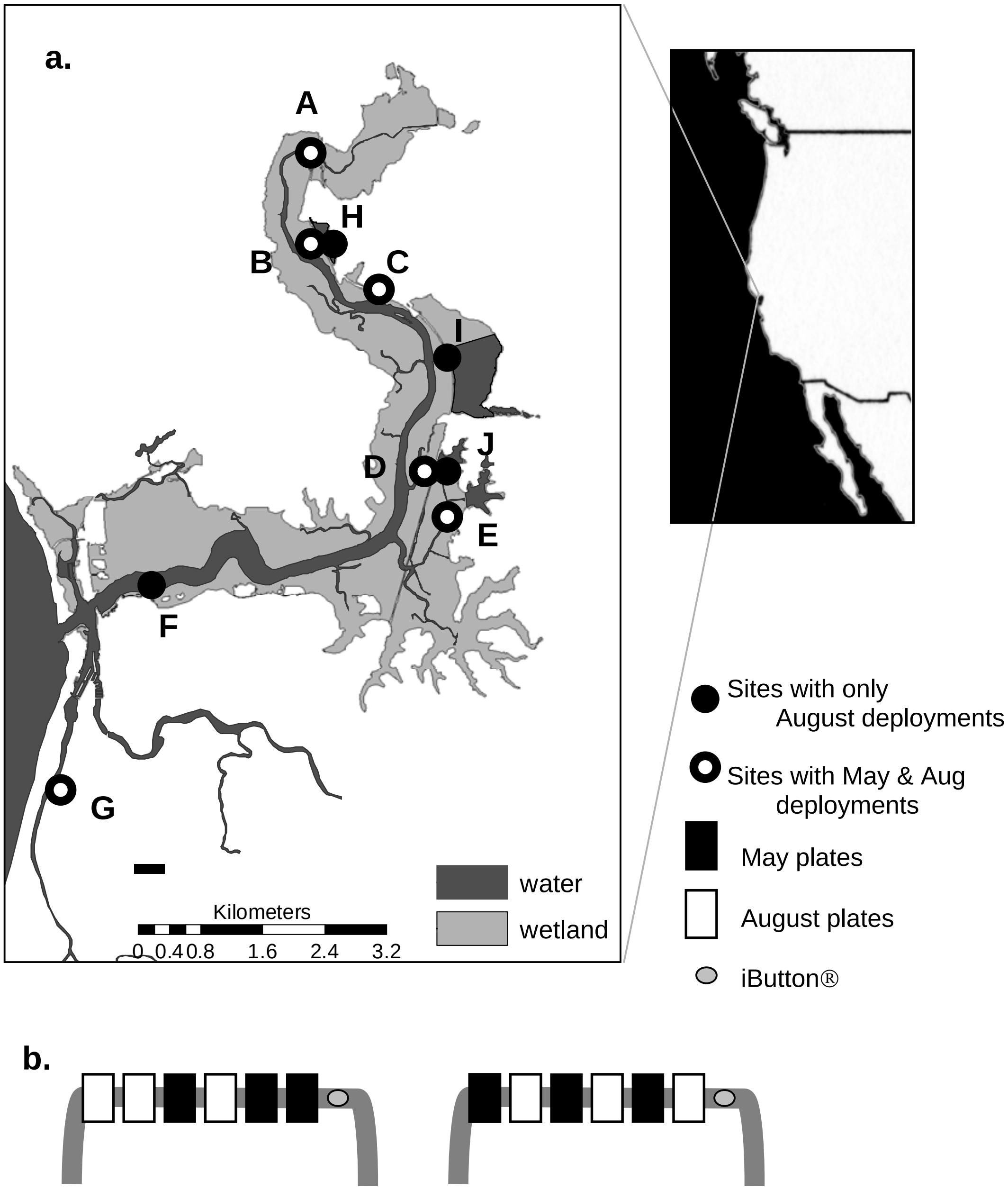
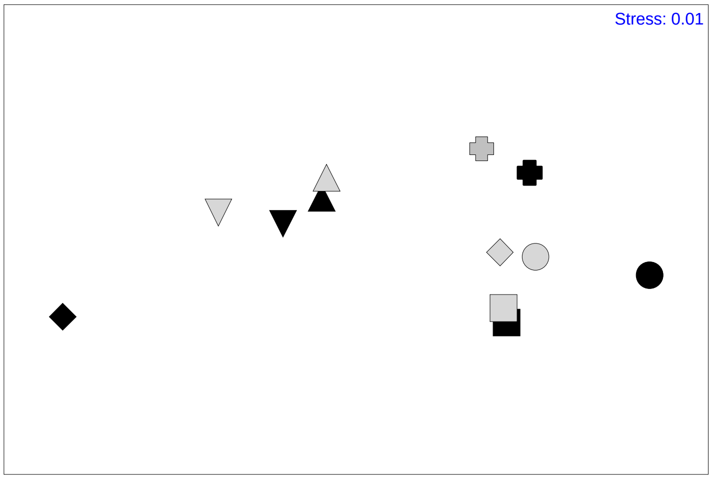


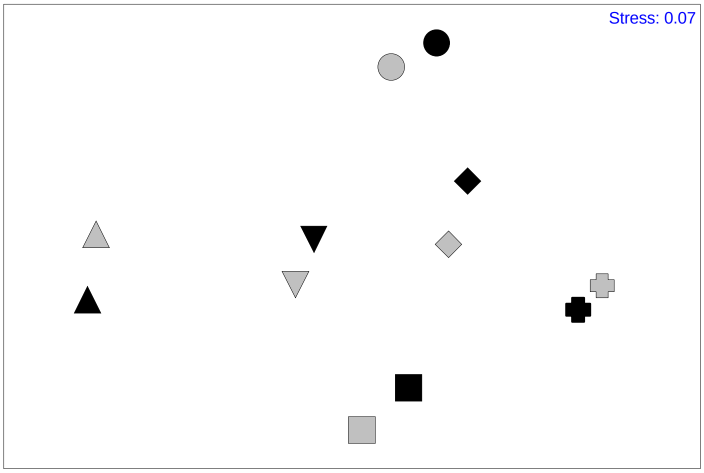
Fig. 2.2 nMDS ordinations of assemblage average percent cover by site and deployment date. a) December 2002, b) October 2004.

a. December 2002



1-way ANOSIM (deployment date) Global *R* = -0.102, *p* = 0.85
1-way ANOSIM (site) Global *R* = 0.672, *p* = 0.001

b. October 2004



1-way ANOSIM (deployment date) Global *R* = -0.141, *p* = 0.89
1-way ANOSIM (site) Global *R* = 1.00, *p* = 0.001

▲ A ▼ B

■ C ◆ D

● E ✚ G

■ Aug deployment (black)

▨ May deployment (gray)

Fig. 2.3 The average monthly percent cover of species at each site displayed by deployment date. X-axis = time (months). Y-axis = avg. % cover. Note, Y-axis scale is from 0-50% for sites A, D, E, 0-2% for site H, and 0-100% for sites B, C, G, F, I, J.

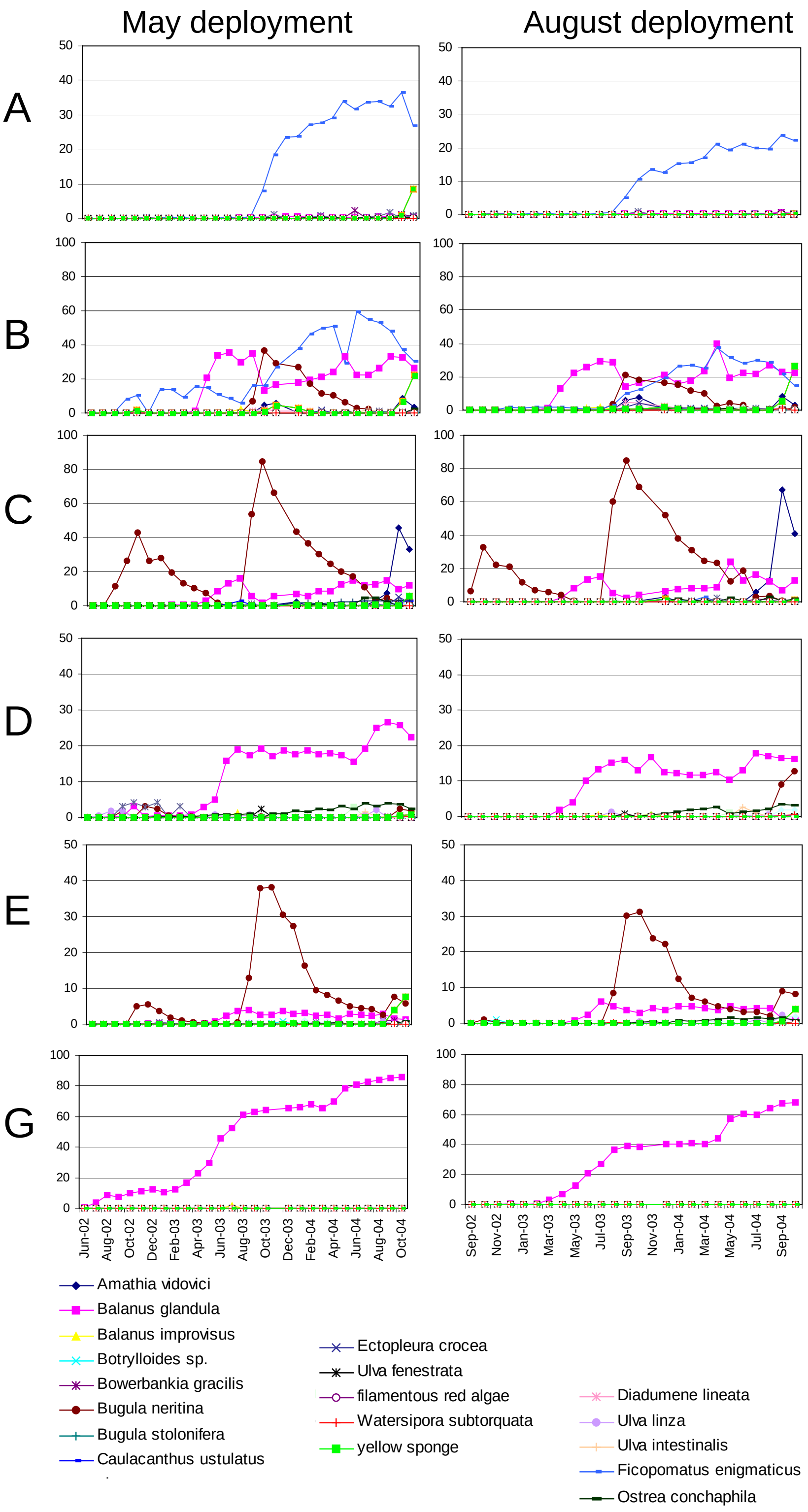


Fig. 2.3 Continued.

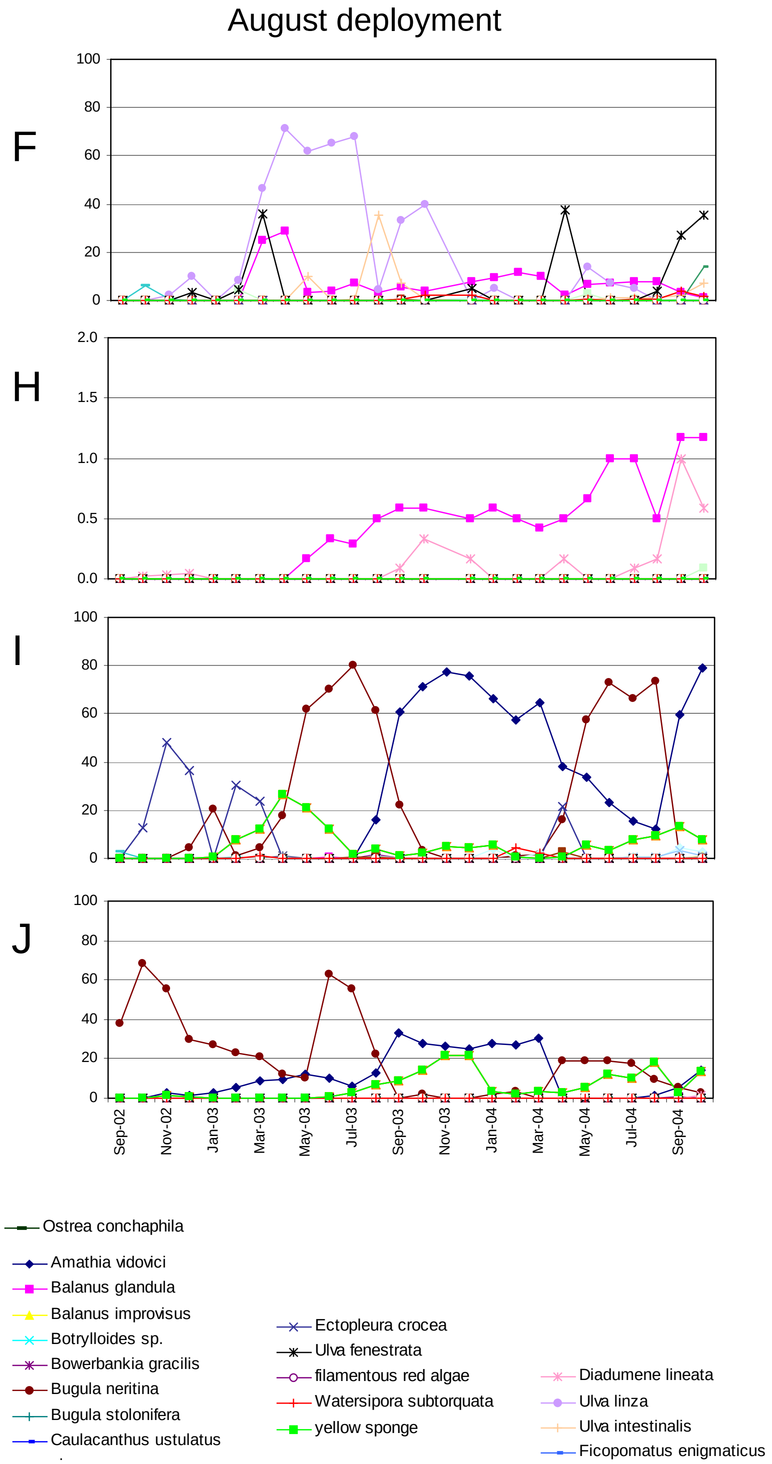
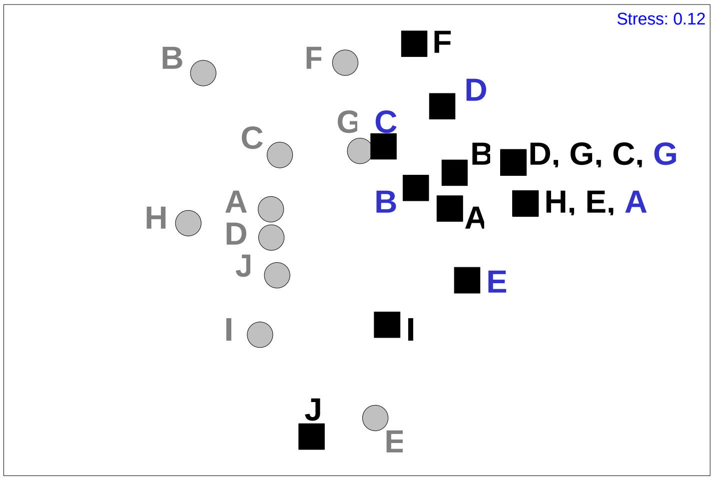


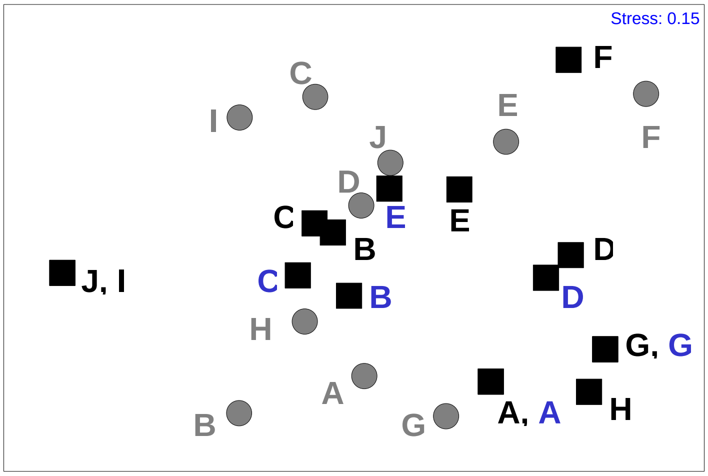
Fig. 2.4 nMDS ordination of assemblages on plates and at sites (based on presence/absence data). a) July 2003, b) December 2003.

a. July 2003



1-way ANOSIM (env vs. plate) Global *R* = 0.565, *p* = 0.001
1-way ANOSIM (site) Global *R* = 0.184, *p* = 0.048

b. December 2003



1-way ANOSIM (env vs. plate) Global *R* = 0.108, *p* = 0.069
1-way ANOSIM (site) Global *R* = 0.502, *p* = 0.001

● Sites ■ Plates (May, Aug)

Fig. 2.5 Cross correlation between the time series of percent cover of *Amathia vidovici* and *Bugula neritina* by site. Gray lines are the 95% confidence intervals.

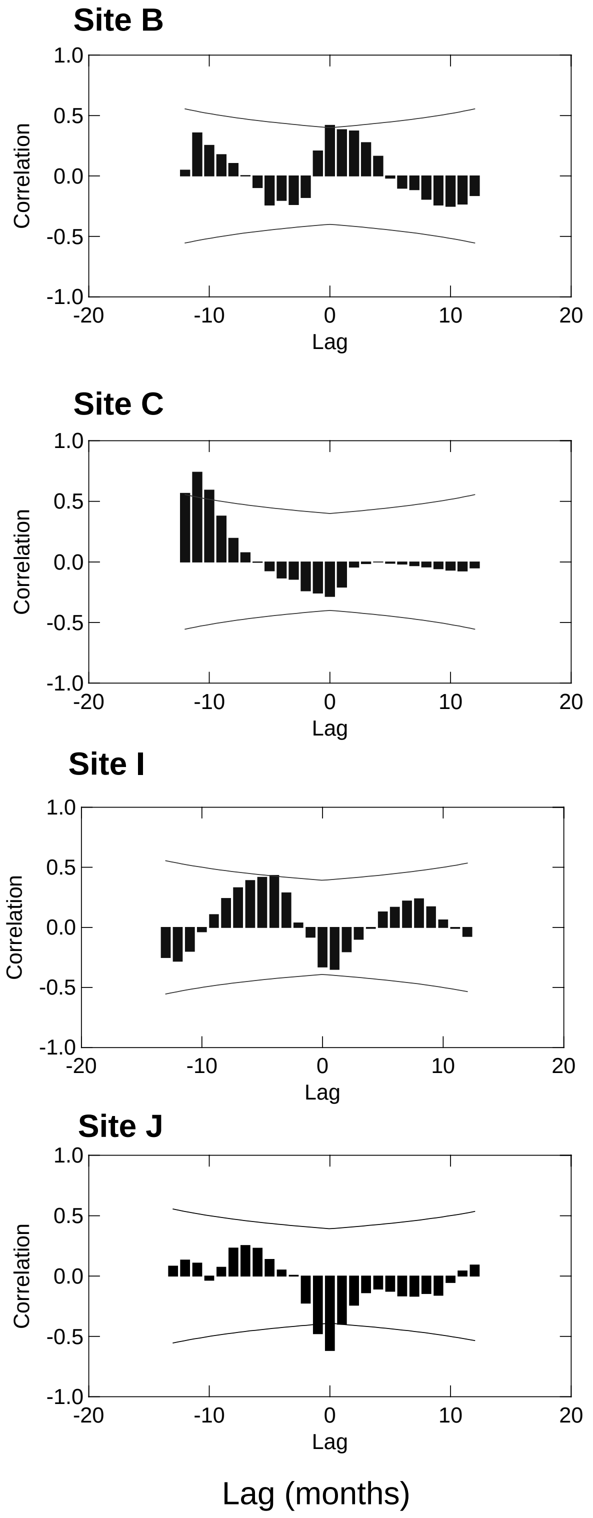
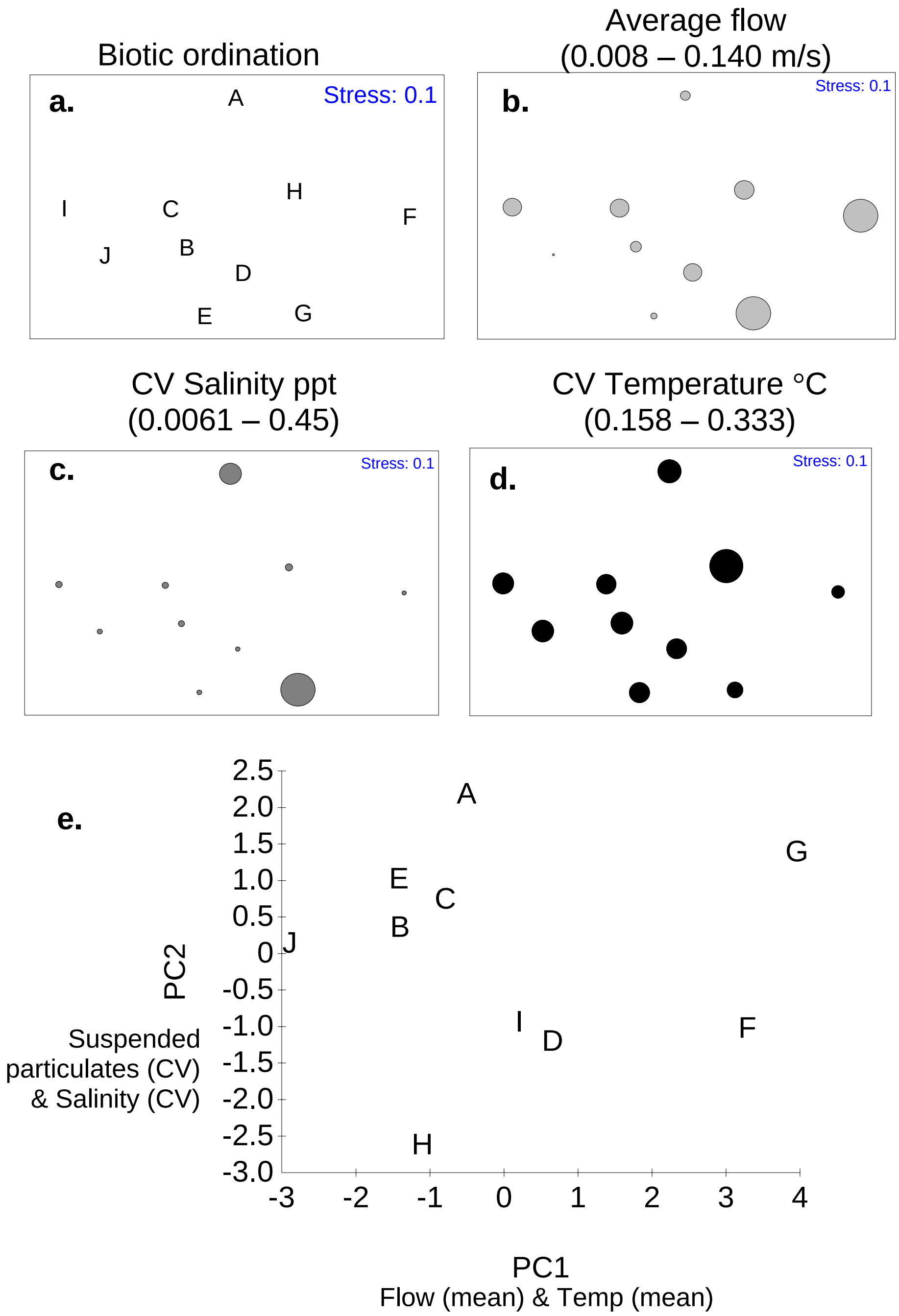


Fig. 2.6 nMDS of average percent cover of assemblages from October 2004 displayed as a) site labels, b) average flow in m/s, c) coefficient of variance of salinity, d) coefficient of variance of temperature. e) PCA of sites based on the coefficient of variance and mean of measured environmental variables summarized in Table 2.2.



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-CHAPTER THREE-

Invasive ecosystem engineer alters infaunal communities in an estuarine environment

ABSTRACT

Many ecosystems are created by the presence of habitat-modifying foundation species. These ecosystem engineers play an important role in determining an environment's species composition. Additionally, the mosaic environment of engineered and non-engineered habitats has been shown to increase biodiversity at large spatial scales. Invasive habitat-modifying species can be introduced into environments without similar, pre-existing ecosystem engineers, resulting in dramatic impacts on native community composition. However, little is known about how invasive ecosystem engineers interact with other non-natives already present in the environment and whether invasive engineers increase local diversity in a manner similar to native ecosystem engineers. In this chapter, I explore the effects of an invasive reef-building tubeworm *Ficopomatus enigmaticus* on the community composition of the central Californian estuary, Elkhorn Slough. The reefs provide habitat for several non-native species, including the amphipods *Monocorophium insidiosum* and *Melita nitida*, which reach densities nearly an order of magnitude higher in the reef matrix than in near-by mudflats. The invasive reefs likely facilitate associated non-natives through habitat provision, enhanced propagule retention and protection from predation. Habitat provision may be a mechanism of invasional meltdown in Elkhorn Slough. Through a reef removal experiment, I show assemblages living in the reefs are significantly different from assemblages in nearby mudflats. Additionally, *F. enigmaticus* reefs alter nearby infaunal assemblages by decreasing the abundance of infaunal species significantly. Once reefs are removed, the newly exposed mudflat is populated by opportunistic non-native species, such as the polychaete *Streblospio benedicti* and *M. insidiosum*. There is some indication that the addition of the invasive reefs to the mudflat environment may enhance local species richness. However, more study is

necessary to understand if this trend for enhanced species richness in areas with both mudflat and invasive reef is a significant and replicable result of the addition of ecosystem engineers to anthropogenically modified environments.

INTRODUCTION

Many ecosystems, such as tropical and riparian forests, savannas, kelp forests, seagrass meadows, coral reefs, and mussel beds are created by the presence of one or more habitat-modifying species. These foundation species (Dayton 1972; Ellison et al. 2005) or ecosystem engineers (Jones et al. 1994, 1997) are defined as species that structure communities by creating locally stable conditions for other organisms and by modulating and stabilizing fundamental ecosystem processes (Dayton 1972). Many species associate with the biogenic structures created by these foundation species and frequently are able to occupy the environment only when the foundation species are present (Dayton 1975; Graham 2004). Ecosystem engineers can facilitate other species by creating habitat, providing refuges from predation, as well as by reducing both physical and physiological stress (Bruno and Bertness 2001). Large-scale habitat modification by foundation species can also facilitate other organisms by increasing propagule retention or the availability of limited resources (Eckman 1985). Positive interactions between foundation species and species that utilize the provided habitat may ultimately be responsible for determining an environment’s species composition (Bruno and Bertness 2001).

While many species benefit from positive interactions with foundation species, some organisms can persist only in an environment that has not been altered by ecosystem engineers (Dayton 1975; Eckman and Duggins 1991). For example, a beaver dam creates a pond in a stream, which decreases stream flow and potentially deprives downstream organisms of needed resources such as oxygen and nutrients. Additionally, the felling of trees for the dams has negative effects on the species living in the trees. For these species the modification of the environment by ecosystem engineers may lead to their local displacement (Jones et al. 1997). However, at larger scales, the mosaic patchwork of engineered and non-engineered environments will provide habitat for species positively and negatively affected by foundation species. The combination of different communities associated with engineered and non-engineered environments may increase species diversity at spatial scales encompassing both environmental types (Jones et al. 1997).

Given the importance of ecosystem engineers for structuring local communities and determining both local and larger-scale diversity patterns, how do communities respond to the introduction of a novel ecosystem engineer? To examine assemblage responses to novel foundation species, I will focus on invasive species. Invasive species are defined as organisms that have been transported by humans into a region not previously occupied and have become established and are causing or likely to cause economic or environmental harm (Carlton 2001). Non-native species are defined as those that fit the above definition but without known detrimental impacts. Some invasive species have the ability to modify recipient environments to such an extent that they become new foundation species for these environments. In a few cases the “native” environments have not been previously exposed to the structuring effects of a similar foundation species. For example, invasive *Spartina* spp. in San Francisco Bay have turned extensive intertidal mudflats into marshes. These marshes have altered infaunal communities and changed geochemical processes (Neira et al. 2005; Brusati and Grosholz *in press*; Levin et al. *in press*). Abundant and dense root mats displace many infaunal organisms while the aboveground shoots decrease light availability to the sediments. The decreased light access reduces benthic algal production and may be responsible in part for the trophic shift of infauna from herbivores to below-ground detritivores (Levin et al. *in press*). The marsh grasses also reduce the amount of foraging and nesting habitat for several species of shore birds, including the endangered California clapper rail, *Rallus longirostris obsoletus* (Toniola et al. 2004). In Coos Bay, Oregon, the invasive seagrass *Zostera japonica* changes sediment characteristics and infaunal abundance when compared to nearby unvegetated areas (Posey 1988). Some common species increase their abundance in the invasive seagrass while other species decline. The community alterations are attributed to an increase in habitat complexity, which shelters many epibenthic species from predation, and to the baffling of currents, which increases filtering ability resulting in increased densities of suspension feeding organisms (Posey 1988). In Mission Bay, San Diego, California the invasive mussel *Musculista senhousia* creates dense mats, which increases infaunal densities, species richness, and densities of a variety of taxa as compared to unpopulated control areas (Crooks and Khim 1999). The physical structure created by the mussel mats is experimentally shown to be responsible for the observed community alterations. However, several planktonic species are inhibited and are rarely if ever found in the mussel mats. The filtration of the water column by the large congregations of filterfeeding invasive mussels is suggested as the possible cause of the decrease in planktonic species in the mussel beds (Crooks and Khim 1999).

In general, research on invasive marine and estuarine foundation species suggests that the physically complex environments created can facilitate many species while simultaneously inhibiting others. What is not yet understood is whether novel invasive ecosystem engineers operate as native ecosystem engineers: increasing larger-scale biodiversity through the creation of a mosaic seascape of engineered and non-engineered environments. Additionally, while many studies have examined the effect of invasive marine ecosystem engineers on community structure, few have asked whether the addition of novel biogenic habitat by invasive species increases the abundance or diversity of other non-native species present in the environment (Grosholz 2005; Brusati and Grosholz *in press*). Due to common historical and modern vectors of non-native species introduction into marine environments (i.e. bivalve aquaculture, boat hull fouling, and rock ballast) many marine non-natives depend on hard substrates during at least some stage of their life (Carlton 1979). Invasive ecosystem engineers frequently increase the abundance of structural resources which may be utilized by other non-native species in the system. The process of non-native species facilitating ongoing and subsequent invasions by increasing the likelihood of survival, population size, and magnitude or extent of ecological impacts of other non-native species is known as an invasional meltdown (Simberloff and Von Holle 1999). In this study, I examine both the local and larger-scale effect of an invasive ecosystem engineer on infaunal communities and explore the possibility of an invasive engineer enhancing the success of other non-native species. I conducted experiments in a central Californian estuary where the reef-building tubeworm *Ficopomatus enigmaticus* has recently established.

Native to Australia, *F. enigmaticus* has been reported in only two locations along the western coast of North America: San Francisco Bay, where it has persisted for 70 years, and Elkhorn Slough, where it has been reported since 1994 (Carlton 1979; Wasson et al. 2001). The tubeworm, *Ficopomatus enigmaticus*, was probably introduced to San Francisco Bay and Elkhorn Slough through boat fouling. In both locations, it has expanded rapidly, with large aggregations of calcareous tubes developing as the larvae gregariously settle on preexisting adult tubes. In Argentina, these tubeworm aggregations, or reefs, have been shown to increase by nearly 10 cm in diameter each year (Schwindt et al. 2004). *F. enigmaticus* reefs can alter flow regimes and sedimentation rates, modifying the physical environment and having direct and indirect effects on benthic communities (Schwindt 1998). In fact, distinct assemblages have been recorded associated with *F. enigmaticus* reefs throughout the world (Thomas and Thorp 1994; Bianchi and Morri 1996; Schwindt and Iribarne 2000; Schwindt 2001). By providing a complex habitat in otherwise structurally simple estuarine mudflats, *F. enigmaticus* reefs could have significant impacts on the physical environment, associated biota, and species interactions within invaded estuaries.

I conducted experimental removals of *F. enigmaticus* reefs to investigate their possible influences on the structure and diversity of benthic invertebrate communities in Elkhorn Slough. Specifically, I addressed the following questions: 1) What, if any, species utilize the invasive habitat? Does *F. enigmaticus* act as a foundation species in its new environment? 2) How does *F. enigmaticus* alter nearby infaunal assemblages in terms of total abundance of fauna, distribution of multiple species, and overall diversity in the mosaic environment of engineered and non-engineered habitats? 3) Is there evidence of an invasional meltdown occurring in this heavily invaded estuary?

METHODS

To determine what species associate with *F. enigmaticus* reefs and evaluate the effects of the reefs on nearby infaunal communities, I conducted a removal experiment at Hudson Landing, in the upper portion of Elkhorn Slough, where extensive reefs are associated with wooden pilings (Fig. 3.1a). Each reef was approximately 1 m in diameter and 0.5 m tall, providing a set of over 100 replicated experimental units. I selected a subset of 12 reefs, located between –0.1 m and 0.1 m MLLW for the experiment. All experimental reefs were sampled before removal, in late May and early December 2002 (see below), by taking two samples through the reef matrix, two cores (10 cm diameter x 10 cm deep) through the underlying sediments, two cores 5 cm away from the reef's edge, and two cores 1 m away from the reef's edge, to sample surrounding mudflat communities. To account for differences in reef sample volume, we standardized associated infaunal abundance by the weight of each reef sample's biogenic hard substrate (the reef material). Cores were sieved to 500 µm in the field, then preserved in 10% formaldehyde solution for fixation, and transferred to 80% ethanol for storage. Samples were sorted under a dissecting microscope. All animals were identified to species and counted. Species were assigned to one of three categories: native, non-native, or cryptogenic (of unknown origin (Carlton 1996)), based on available studies (Carlton 1979; Ruiz et al. 2000; Wasson et al. 2005).

Following sampling, four reefs were completely removed and four were not manipulated and served as controls (Fig. 3.1b). To evaluate possible effects of experimental disturbance, four additional reefs were removed then returned to their original locations. The reefs were broken away from the piling with shovels. For complete removal all reef material was scraped from the piling, collected in large plastic tubs, and disposed of in the terrestrial environment. To establish removal controls, a boogie board was wedged under the reef before the reef was broken away from the piling. Careful prying with the shovel allowed large chunks of the reef to break off. The reef pieces were then dragged at least 1 m away from the piling on the boogie board. The boogie board was then pushed back toward the piling, and the reef fragments were slid carefully back into place around the piling. See pictures in Fig. 3.1b for photographs of the reef treatments.

To address possible seasonal differences in community responses to reef removal, experimental removals occurred on two dates, in summer (May 27th) and winter (December 2nd) of 2002. Following reef removal, sampling was repeated as described above six months and one year after treatment. On these sampling dates, reef samples were collected only from the remaining reefs (i.e., the undisturbed reefs and the disturbance control reefs). When reefs were removed, only sediment cores were collected. Finally, to understand how infaunal communities near the reef differed from communities not previously exposed to the reefs, 8 infaunal cores from a mudflat in the same general vicinity, but at least 20 m from all *F. enigmaticus* reefs, was collected on each one year post-treatment sampling date.

I hypothesized that reefs influence sediment grain size distribution by baffling currents and increasing particle deposition, and enhance organic content in the sediment through the accumulation of *F. enigmaticus* fecal material. Grain size characteristics as well as sediment organic content are known to influence infaunal communities (Rhoads 1974; Jumars 1975). If *F. enigmaticus* does indeed modify these environmental characteristics, then this may be a mechanism by which infaunal communities near reefs are altered. To determine whether reefs alter the nearby physical environment by modifying sedimentation rates and deposition of organic matter, two sediment samples (5 cm diameter x 5 cm deep) were taken near each infaunal core. One of the sediment samples was used for sediment size analyses and the other to determine sediment organic content. Proportions of sediments within different grain size classes were quantified for summer before and 1 year post-treatment samples using standard wet sieving and pipette analyses outlined in Folk (1980). Proportions of organic matter in the sediments were quantified by drying samples at 60°C, then incinerating organics at 500°C in a muffle furnace and determining weight losses (Folk 1980). One sample from each distance for each reef was analyzed for percent organics.

To assess the effects of non-native reefs on the benthic communities living in the nearby mudflat environments, I conducted univariate and multivariate analyses of the animal counts from sediment cores. Invertebrate abundances and percent non-natives within cores were compared among experimental treatments and dates using nested analysis of variance (ANOVA) models with experimental treatment (removal, control, disturbance control), removal season (summer, winter), time of sampling (before removal, six months, and one year after removal), and location relative to reefs (under the reef, 5 cm, and 1 m away) as fixed factors.

Reefs are a random factor nested within the treatment by season interaction. Dunn-Šidák corrections were used to adjust significance levels to account for the two different ANOVA tests (Sokal and Rohlf 1995). Multivariate analyses, including ordinations and randomization tests, were used to examine effects of reef removal on the composition of invertebrate assemblages. Bray-Curtis dissimilarity (Bray and Curtis 1957) between pairs of samples was calculated on square-root transformed abundances to reduce the influence of the most common species on community dissimilarity. A 1-way Analysis of Similarity (ANOSIM) with treatment as the factor was conducted for each separate date and season (Clarke and Warwick 1994). To identify community differences between reef and mudflat habitats, a 1-way ANOSIM with location as the factor was conducted for all samples. The taxa contributing to observed differences between groups of samples were identified using similarity percentage (SIMPER) analyses (Clarke and Warwick 1994). Multivariate analyses were performed using the statistical package PRIMER v.5 (PRIMER-E Ltd, Plymouth, UK).

To understand how the reefs affect seascape level diversity, I calculated abundance-based species richness using classic ACE estimation for each reef unit (defined as the two reef samples when available, two under, two 5 cm, and two 100 cm away infaunal cores collected from each experimental reef) (Magurran 2004). I then compared species richness estimates for each reef unit across treatments and time. If the presence of the reef enhances local diversity, then there should be a significant treatment by time interaction, with reef removal reducing local diversity by the end of the experiment. The ANOVA model of this analysis uses the three orthogonal factors: treatment (control, disturbance control, and removal), season (summer and winter), and time (before removal, six months, and one year after removal).

Percent organics in the sediment samples was compared across treatments with the following ANOVA model: season, time, treatment, and distance as fixed orthogonal factors. To examine the effects of reefs on percent of fines and sands in the sediment samples, I used an ANOVA model with the fixed factors time (before removal and one year after removal), treatment, and location. Dunn-Šidák corrections adjusted significance levels to account for the two separate ANOVA tests, one for fines (<60 µm) and one for sands (>60 µm) (Sokal and Rohlf 1995). Due to the time consuming nature of wet sieving, I limited this analysis to summer samples from before removal and one year after removal.

RESULTS

Twenty-eight species were identified in the 288 core infaunal and reef samples processed for this study. Of the 137,746 organisms identified, 55,338 were found associated with the reef structure and 82,407 were found in the nearby mudflats, illustrating that many organisms utilize the invasive reef habitat. The assemblages within and around reefs had high abundances of non-natives, with 78.5% (108,174) of the organisms identified as non-native to Elkhorn Slough. This proportion was greater in reef samples (95.5%) as compared to mudflat samples (64.3%) (Fig. 3.2). Most of the species were found in both habitats but exhibited greater abundances in either the mudflat or the reef environment. Only a few rare species were found exclusively in one environment (Table 3.1). Even with the relative lack of environmental specificity observed in the species from this study, the assemblages living in the reefs had a significantly different composition than assemblages found in any of the mudflat locations (1-way ANOSIM global $R = 0.432$, $p = 0.001$; Fig. 3.3). The differences in assemblage composition were driven by highly abundant invasive amphipods *Monocorophium insidiosum* and *Melita nitida* in the reefs and the abundant invasive polychaete *Streblospio benedicti* and native oligochaete *Thalassodrilides gurwitschi* in the mudflats.

Ficopomatus enigmaticus reefs affected total faunal abundance in nearby mudflats, but the effects varied with sampling date and season (ANOVA: season × time × treatment interaction $F = 5.5$, df = 4 & 12, $p = 0.0094$) (Table 3.2). There was an increase in infauna in the mudflats exposed by reef removal, primarily due to an increase in the abundance of the non-native polychaete *Streblospio benedicti*, the non-native amphipod *Monocorophium insidiosum*, and the native oligochaete *Thalassodrilides gurwitschi* (Fig. 3.4b, c, e). This is particularly apparent when removals were conducted in the summer, where this pattern is present six months and one year after removal. With the winter removals, the increase in abundance of infauna in exposed mudflats is apparent six months but not one year after reef removal. Both before and after removals, there is a trend for more abundant infauna in samples 100 cm away from reefs (Fig. 3.2, Fig. 3.4a, d, c, e).

Reef removals had significant effects on community structure in nearby mudflats. Results of multivariate analyses are summarized here by reporting *R*-values from analysis of similarity randomization tests (ANOSIM) comparing the structure of infaunal assemblages among treatments and distances. *R* compares the average rank dissimilarity within and between groups of samples and can be compared across different ANOSIM analyses (Clarke and Warwick 1994). The greater the *R*-value for a particular factor comparison (e.g. treatment groups), the greater the similarity of samples within these two groups versus between the groups (i.e. the more variance in assemblage structure is explained by that particular factor, in this case treatment group). ANOSIM reveals no significant difference between assemblages before treatment (summer global $R = -0.08$, $p = 0.838$; winter global $R = 0.048$, $p = 0.227$). Six months after treatment, removals are significantly different from controls within the summer experiment, ($R = 0.264$, $p = 0.032$; Fig. 3.5a), but not in the winter experiment ($R = 0.094$, $p = 0.189$; Fig. 3.5b), whereas assemblages from removal samples are significantly different from disturbance controls in both summer and winter treatments (summer $R = 0.347$, $p = 0.005$; winter $R = 0.267$, $p = 0.035$; Fig 3.5a, b). These observed assemblage responses persist through time, with removals significantly different from both disturbance controls and controls one year after treatment, regardless of the season in which the experiment was initiated (summer global $R = 0.183$, $p = 0.017$; winter global $R = 0.316$, $p = 0.001$ Fig. 3.5a, b). These patterns of assemblage responses are determined in part by an increase in the abundance of the non-native amphipod *Monocorophium insidiosum* in removal samples, and an increase in the abundance of the oligochaetes *Thalassodrilides gurwitschi* (native) and *Tubificoides brownae* (non-native) in control and disturbance control samples.

Species richness did not appear to be affected by the presence of invasive reefs. There were 12 to 21 species associated with each reef unit (i.e., each individual reef and the nearby mudflat environment, sampled underneath, 5 cm, and 100 cm away from each reef) on individual sampling dates. When species richness per reef unit was tested for response to experimental treatment in the 3-way ANOVA described above, there were no significant interactions, but time (*F* = 7.09, df = 2 & 18, *p* = 0.0054) and season were both significant factors (*F* = 13.15, df = 1 & 18, *p* =0.0019), and treatment was nearly significant (*F* = 3.43, df = 2 & 18, *p* = 0.0547) (Table 3.3). Before and six months after the summer experiment, species richness in removal reef units was significantly less than in controls (Fig. 3.6a). However, there was no difference between the treatment groups, one year post-removal. Species richness in removal reef units was almost identical to disturbance controls in the winter experiment regardless of sampling date, with control reef units having higher species richness six months and one year after treatment (Fig. 3.6b).

The analysis of sediment grain size did not show any treatment effect (ANOVA, sands *F* = 1.89, df = 2 & 18, *p* = 0.1803; fines *F* = 0.92, df = 2 & 18, *p* = 0.4180). However, the amount of sands and fines in the sediment samples varied significantly with distance from reef (ANOVA, sands *F* = 16.48, df = 2 & 18, *p* = 0.0001; fines *F* = 11.49, df = 2 & 18, *p* = 0.0006) and sampling time (ANOVA, sands *F* = 25.43, df = 2 & 18, *p* = 0.0001; fines *F* = 19.12, df = 2 & 18, *p* = 0.0004) (Table 3.4). The later sampling dates, regardless of treatment, had greater sand content as compared to the earlier sampling dates (Fig. 3.7). Sand content was also high near and under reefs and decreased with distance from reefs (Fig. 3.7a, c). Fine content in sediment samples showed the opposite pattern, increasing with distance from reefs and decreasing with time (Fig. 3.7b, c).

In contrast to sediment grain size, sediment percent organics had significant season × treatment (ANOVA *F* = 5.81, df = 2 & 54, *p* = 0.0127) and season × time (ANOVA *F* = 16.5, df = 2 & 54, *p* = 0.00001) interactions (Table 3.5). In the winter experiment, sediment samples from removal treatments had consistently lower percent organics than the disturbance control and the control samples. Organic content of the sediment samples also increased with time regardless of the season when the experiment was initiated or experimental treatment, with the highest organic contents observed one year after experimental manipulation in both the summer and winter treatment (Fig. 3.8).

There was no significant treatment effect on the percent of non-native species in the mudflats adjacent to the invasive reefs. However, the four-way interaction term season × time × treatment × distance is nearly significant ($F = 2.72$, df = 8 & 108, $p = 0.0273$). This nearly significant interaction seems to be driven by a trend for increased percentage of non-natives in the removals in winter treatments which is more pronounced in the under and 5 cm samples than in the 100 cm samples (Fig. 3.9). An increase in the abundance of the non-native polychaete *Streblospio benedicti* and the non-native amphipod *Monocorophium insidiosum* is responsible for the observed increase in non-native species in these samples. The ANOVA for the percentage of each sample comprised of non-native species has two significant interaction terms after Dunn-Šidák corrections: time x reef ($F = 3.84$, df = 12 & 108, $p = 0.0001$) and season × time ($F = 8.21$, df = 2 & 12, $p = 0.0057$) (Table 3.2). This is partially explained by the trend for winter samples to have lower percent non-natives as compared to summer samples (Fig. 3.2, Fig. 3.9), and for the highly variable between reef percent non-natives before and 6 months after treatment in the winter experiment (Fig. 3.9d, e).

DISCUSSION

Ficopomatus enigmaticus produces reefs that are structurally stable over time (personal observation), providing complex 3-dimensional habitat in a soft sediment environment. This habitat hosts an abundant associated fauna, distinct from nearby mudflats in relative abundance of species and, to a lesser extent, species composition. Thus *F. enigmaticus* can be considered a foundation species (Dayton 1972) or ecosystem engineer (Jones et al. 1994), which enhances local abundances of associated organisms. The most abundant species associating with the non-native reefs are themselves non-native, implying that *F. enigmaticus* may facilitate these non-natives, increasing their abundance locally and leading to an “invasion meltdown” (Simberloff and Von Holle 1999). In addition to providing habitat for species directly associated with these biogenic structures, non-native reefs also influence communities living in nearby mudflats by decreasing infaunal abundance and altering assemblage structure. However, it is unclear whether this ecosystem engineer increases larger-scale species richness.

The highly abundant assemblages associated with the non-native reefs are significantly different from assemblages in nearby and distant mudflats. The same suite of common species found in the reefs is also found in the nearby mudflats, suggesting that there are no strictly obligatory relationships between the reefs and any of the commonly associated species. The only species to be found either in the reefs or in the mudflat but not in both locations are rare species. Assemblage composition but not structure may be similar between the two habitat types because the assemblage contains few species and is dominated by small mobile generalists. Many of the species are non-native and may become successfully established in the system because of their capability for living under a broad range of conditions. Differences in relative abundances, however, suggest that recruitment and survival of some of these generalists differ between the two habitat types.

There are a number of general facilitative mechanisms attributed to ecosystem engineers, which could enhance recruitment and survival of associated species in the non-native ecosystem engineer's reef matrix. The reefs, which are complex intertwined tube structures, may provide shelter from predators such as shore birds and fish. These predators may not be able to access the spaces between tubes within the reefs due to the complex geometry of the reefs. The reefs may also increase propagule retention, as the two most common reef associated amphipods, *Monocorophium insidiosum* and *Melita nitida*, brood their young (Nair and Anger 1979; Borowsky 1980). These juvenile amphipods are already within the reefs, increasing the local abundance of these species without the need for immigration from external sources. To identify the exact facilitation mechanisms, further research is necessary.

Through experimental reef removals, I found that the presence of reefs displaces infaunal communities, resulting in decreased abundances near reefs and higher abundances away from the edges of reefs. When reefs are removed, there is a rapid colonization of the exposed mudflat by opportunistic species such as the non-native polychaete *Streblospio benedicti* and the native oligochaete *Thalassodrilides gurwitschi*. The reefs' impact seemed to be limited spatially to communities under and adjacent (within 5 cm) to the edges of reefs. Reefs could cause a local decrease in infaunal abundances through a number of mechanisms. Water filtration by the reef-building *F. enigmaticus* may limit the availability of food resources to infaunal filterfeeders such as *Streblospio benedicti*, *Polydora socialis* and *Boccardia* species. Davies and colleagues measured the filtration rate of a *F. enigmaticus* population in Marina da Gama, Zandvlei, South Africa, and noted that it was substantial (8.59 ml mg^{-1} worm h^{-1}) (Davies et al. 1989). The standing stock could filter all of the water in this South African marina in just over 26 hours (Davies et al. 1989). With the large congregations of reefs in the northern section of Elkhorn Slough, it is likely that *F. enigmaticus* could be having dramatic effects on the abundance of food suspended in the water column. Conversely, accumulations of fecal material may provide food to infaunal detritivores. An alteration in the amount of detritus in local environments has been implicated in community alterations associated with other non-native habitat modifying species such as Zebra mussels, the Asian mussel *Musculista senhousia*, and *Spartina* marsh grasses (Stewart and Haynes 1994; Crooks and Khim 1999; Neira et al. 2005; Levin et al. *in press*). My analysis of sediment organics supports this supposition, with winter removal sediments having consistently lower percent organics. However, the sediment data should be interpreted with caution because winter removal samples had lower organics before experimental treatment indicating that the observed pattern may be due to initial organic levels not treatment effects. Additionally, a similar pattern of decreased organics in removal samples was not observed in the summer experiment. Changes in sediment grain size did not explain observed patterns of community responses to reef removal. Sediment gain size did not show an effect of treatment but rather sands increased and fines decreased with time regardless of treatment. This is most likely due to the continued accumulation of reef fragments in the muddy substrate over time. When reefs were removed, reef debris was added to the substrate, possibly preventing detection of a removal signal.

Ficopomatus enigmaticus reefs may indirectly structure local infaunal communities by harboring predators or scavengers feeding on fauna or causing physical disturbance in the surrounding environment. Impacts of *F. enigmaticus* reefs on associated invertebrate communities through biotic interactions were documented in the Mar Chiquita Coastal Lagoon, Argentina. In the Argentinean system, *F. enigmaticus* reefs attract and support high densities of the predatory native crabs, *Crytograpsus* *angulatus*. Increased predation by crabs on epifaunal and infaunal invertebrates caused significant changes in mudflat communities within a 20 cm “halo” around the reef’s edge (Schwindt 2001). The *F. enigmaticus* reefs in Elkhorn Slough show a similar spatial influence on infaunal assemblages as well as supporting high densities of the native shore crab, *Hemigrapsus oregonensis*. Unlike the Argentinean system, *H. oregonensis* is an omnivore, feeding mostly on algae and diatoms but consuming meat when available (Morris et al. 1980). However, *H. oregonensis* is a good digger and may structure infaunal communities around the reefs by frequent excavations increasing disturbance of local sediments.

It is not clear from the results of this experiment whether the biogenic habitat created by *F. enigmaticus* reefs enhance species richness on larger-scales. The analysis of species richness across mosaic engineered and non-engineered habitats did not illustrate a significant increase, but rather a trend for an increase, in species richness with the increase in habitat heterogeneity through the addition of invasive reefs. This lack of a significant increase in species richness may be attributed to the organically-enriched species-poor environment where the reefs were found. Most of the organisms in this study were opportunistic generalists capable of living in many different environments. Similar species depauperate opportunistic assemblages are observed in other anthropogenically disturbed terrestrial, freshwater, and marine environments. Further analysis is needed to address the possibility that ecosystem engineers invading anthropogenically disturbed habitats may not increase diversity on a scale ecologically relevant to associated species.

There is no indication that the presence of the invasive reefs alters the percentage of non-natives in the nearby infaunal environment. Additionally, the presence of reefs appears to decrease both native and non-native infaunal abundance in mudflats under and adjacent (5 cm away) to the reefs, providing no indication that reefs facilitate non-native mudflat communities. However, the highly abundant non-native species associated with the non-native reefs suggest the possibility of positive interactions between associated non-native species and the invasive reef itself. The non-native reefs provide resources, which are otherwise limited in mudflat environments, namely hard substrate habitat, to non-natives such as *Monocorophium insidiosum* and

Melita nitida introduced to the system through association with hard substrates like oyster spat or boat hulls (Wasson et al. 2001). These two common vectors of introduction into Elkhorn Slough may have selected for a suite of species that associate preferentially with hard substrates during some phase of their lives. A comparison of non-native species that are believed to be introduced to Elkhorn Slough through these mechanisms (Wasson et al. 2001) and the species found to have greater abundance in the reefs than in the mudflats (Table 3.1) shows that for some species (such as *M. insidiosum, M. nitida, Sinolobus stanfordi*) this may be true. For these species, the provision of limited resources by the non-native tubeworm may be a mechanism of invasion meltdown in this system. However, some species believed to have been introduced through associations with hard substrate were more abundant in the mudflat environment (e.g. *Streblospio benedicti, Grandidierella japonica* and *Gemma gemma*). Most species introduction has been attributed to more than one vector. Even when there is only one introduction vector, knowing a species was introduced in association with hard substrates does not indicate whether the species is dependent on hard substrates. For example, *S. benedicti* and *G. gemma* are known infaunal organisms that can associate with hard structures such as oyster shells but are also common in mudflats. Information beyond proposed introduction vectors is needed to understand why some non-natives are found frequently associated with the reefs and others with the mudflats.

Non-native ecosystem engineers establishing in disturbed environments may play different engineering roles than native ecosystem engineers. Instead of facilitating the species that evolved in a particular habitat, they may enhance the abundance, and possibly the diversity, of associated non-native species. The habitat creation by non-native ecosystem engineers may represent one mechanism for invasional meltdown. However, the facilitation appears to be limited to non-native species that associate with the non-native structure itself, as the reefs have a negative but spatially limited impact on both the native and non-native components of local infaunal assemblages.

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Table 3.1 List of all species identified in this study. Total abundance: number of individuals across all samples (n=288 samples). * Percent reported after standardizing by amount of reef material. ** N = native, I = introduced or non-native, C = cryptogenic (of unknown origins (Carlton 1996)). Organisms not identified to species were not categorized as N, I, or C.

	Phylum	total abundance	total in reefs (n=56)	total in mudflat (n=232)	% in reef *	% in mudflat *	native/ introduced **
Monocorophium insidiosum	Arthropoda	54,090	38,103	15,987	90.8	9.2	I
Streblospio benedicti	Annelida	23,387	374	23,013	6.3	93.7	I
Thalassodrilides gurwitschi	Annelida	22,015	557	21,458	9.7	90.3	N
Melita nitida	Arthropoda	14,109	13,487	622	98.9	1.1	I
Tubificoides brownae	Annelida	9,285	407	8,878	16.0	84.0	I
Grandidierella japonica	Arthropoda	6,433	140	6,293	8.4	91.6	I
Capitella capitata	Annelida	4,023	143	3,880	13.2	86.8	C
Hemigrapsus oregonensis	Arthropoda	1,391	1,286	105	98.1	1.9	N
Polydora socialis	Annelida	927	435	491	78.6	21.4	N
Gemma gemma	Mollusca	436	5	431	4.6	95.4	I
Nebalia gerkenae	Arthropoda	375	34	341	29.2	70.8	N
Sinolobus stanfordi	Arthropoda	301	286	15	98.7	1.3	I
Boccardia hamata	Annelida	283	1	282	1.4	98.6	N
Eteone californica	Annelida	238	13	225	19.3	80.7	N
Heteromastus filiformis	Annelida	119	0	119	0.0	100.0	I
Allorchester angusta	Arthropoda	93	35	58	71.4	28.6	N
Harpacticoid copopods	Arthropoda	59	0	59	0.0	100.0	
Syllidae	Annelida	31	1	30	12.1	87.9	N
Leptochelia dubia	Arthropoda	19	2	17	32.8	67.2	N
Notonectidae or Corixidae	Arthropoda	18	0	18	0.0	100.0	
Ammonia beccarii	Rhizopoda	17	0	17	0.0	100.0	N
Cirratulus cirratus	Annelida	16	7	9	76.3	23.7	N
Sphaeroma quoyanum	Arthropoda	16	13	3	94.7	5.3	I
Boccardia proboscidea	Annelida	12	1	11	27.4	72.6	N
Heptacarpus kincaidi	Arthropoda	11	0	11	0.0	100.0	N
Batillaria attramentaria	Mollusca	9	3	6	67.4	32.6	I
Alderia modesta	Mollusca	8	1	7	37.2	62.8	N
Ostracod	Arthropoda	8	1	7	37.2	62.8	
Polydoria ligni	Annelida	5	1	4	50.9	49.1	I
Calanoid copopod	Arthropoda	4	1	3	58.0	42.0	
Ianiropsis tridents	Arthropoda	3	0	3	0.0	100.0	N
Maera simile	Arthropoda	2	0	2	0.0	100.0	N
Cumella vulgaris	Arthropoda	1	0	1	0.0	100.0	N
Ampithoe	Arthropoda	1	1	0	100.0	0.0	
Exoinonata Isopod	Arthropoda	1	0	1	0.0	100.0	
Total		137,746	55,338	82,407			

Table 3.2 ANOVA results for total abundance of organisms in infaunal samples and percent non-natives in infaunal samples. With Dunn-Šidák correction, factors and interactions are significant below *p* = 0.0253.

		total abundance			**% non-natives**		
Source	df	MS	F	*p*	MS	*F*	*p*
season [se]	1	27.77	0.3	0.6030	9938.26	8.11	**0.0293**
time [ti]	2	145.64	5.22	**0.0234**	277.93	0.71	0.5124
treatment [tr]	2	38.30	0.42	0.6777	1649.81	1.35	0.3288
reef (se × tr) [re]	6	92.21	3.15	**0.0069**	1225.34	11.98	**0.0000**
distance [di]	2	590.29	16.15	**0.0004**	466.81	4.62	0.0325
se × ti	2	1753.98	62.81	**0.0000**	3226.30	8.21	**0.0057**
se × tr	2	26.91	0.29	0.7569	506.72	0.41	0.6788
se × di	2	0.61	0.02	0.9832	66.48	0.66	0.5356
ti × tr	4	61.20	2.19	0.1316	472.83	1.2	0.3592
ti × re (se × tr)	12	27.93	0.95	0.4969	392.89	3.84	**0.0001**
ti × di	4	5.68	0.16	0.9547	77.95	0.96	0.4460
tr × di	4	40.79	1.14	0.3836	75.35	0.75	0.5792
di × re (se × tr)	12	35.75	1.22	0.2778	101.04	0.99	0.4656
se × ti × tr	4	153.54	5.5	**0.0094**	568.33	1.45	0.2784
se × ti × di	4	109.30	3.15	0.0325	64.30	0.79	0.5407
se × tr × di	4	2.07	0.06	0.9929	101.19	1	0.4443
ti × tr × di	8	52.42	1.51	0.2058	133.40	1.65	0.1637
di × ti × re (se × tr)	24	34.71	1.19	0.2711	80.98	0.79	0.7400
se × ti × tr × di	8	59.58	1.72	0.1458	220.41	2.72	0.0274
RES	108	29.27			102.32		
TOT	215						

Table 3.3. ANOVA table for abundance-based species richness per reef unit. (Species richness from classic ACE estimators.)

		total abundance		
Source	df	MS	F	*p*
season [se]	1	235.52	13.15	**0.0019**
time [ti]	2	126.99	7.09	**0.0054**
treatment [tr]	2	61.44	3.43	0.0547
se × ti	2	33.55	1.87	0.1824
se × tr	2	45.26	2.53	0.1079
ti × tr	4	30.05	1.68	0.1990
se × ti × tr	4	30.15	1.68	0.1978
RES	18	17.92		
TOT	35			

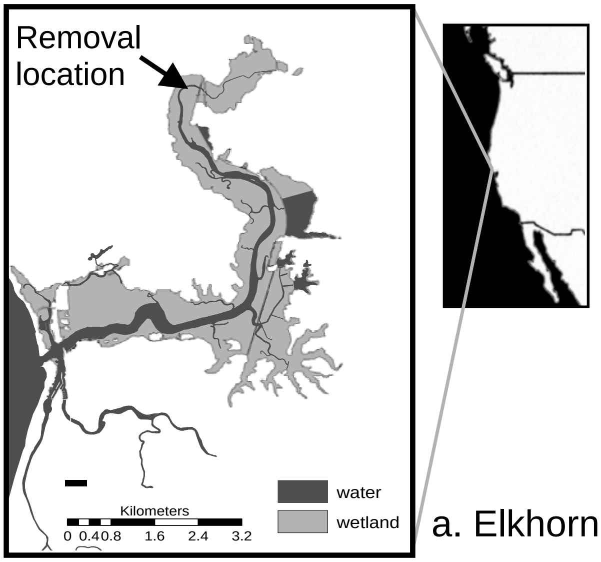
Table 3.4 ANOVA table for sediment grain size results. The first series of columns summarize results for sands and the second for fines. With Dunn-Šidák corrections, factors and interactions are significant below *p* = 0.0253.

		sands			**fines**		
Source	df	MS	F	*p*	MS	F	*p*
time [ti]	1	36.15	25.34	**0.0001**	50.28	19.12	**0.0004**
treatment [tr]	2	2.69	1.89	0.1803	2.41	0.92	0.4180
distance [di]	2	23.51	16.48	**0.0001**	30.22	11.49	**0.0006**
ti × tr	2	3.36	2.36	0.1233	3.93	1.5	0.2507
ti × di	2	0.86	0.6	0.5584	5.60	2.13	0.1478
tr × di	4	0.67	0.47	0.7569	1.94	0.74	0.5782
ti × tr × di	4	0.73	0.51	0.728	1.47	0.56	0.6949
RES	18	1.43			2.63		
TOT	35						

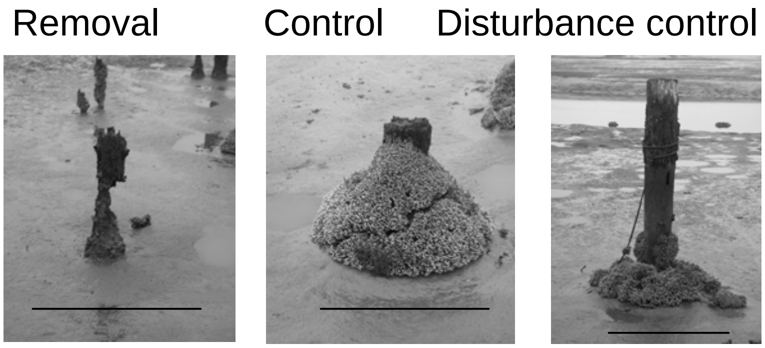
Table 3.5 ANOVA results for analysis of percent organics in sediments.

		total abundance		
Source	df	MS	F	*p*
season [se]	1	187.89	153.15	**0.00001**
time [ti]	2	229.91	187.4	**0.00001**
treatment [tr]	2	7.30	5.95	**0.0046**
distance [di]	2	15.31	12.48	**0.00001**
se × ti	2	16.50	13.45	**0.00001**
se × tr	2	5.81	4.74	**0.0127**
se × di	2	1.96	1.59	0.2126
ti × tr	4	1.91	1.56	0.1989
ti × di	4	1.38	1.13	0.3531
tr × di	4	1.97	1.61	0.1856
se × ti × tr	4	2.08	1.7	0.1639
se × ti × di	4	0.30	0.25	0.9111
se × tr × di	4	0.57	0.46	0.7635
ti × tr × di	8	0.53	0.44	0.8942
se × ti × tr × di	8	0.86	0.7	0.6899
RES	54	1.23		
TOT	107			

Fig. 3.1 a) Map of Elkhorn Slough with persistent waterway represented in dark gray and wetlands in light gray. Arrow identifies the location of removal experiment. b) Pictures of reefs from different experimental treatment groups. Lines on photographs represent 1m.



a. Elkhorn Slough



b. Experimental treatments

Fig. 3.2 The abundances of natives (hashed) and non-natives (solid) at different sampling locations and dates. Abundances are averaged from before samples. Summer samples are in black and winter in gray. Reef abundances are averaged after standardization by reef material sampled. ^ “20m” are averages of 8 cores from the reference mudflats collected 1 year after all other samples but from the same season (see methods for further details).

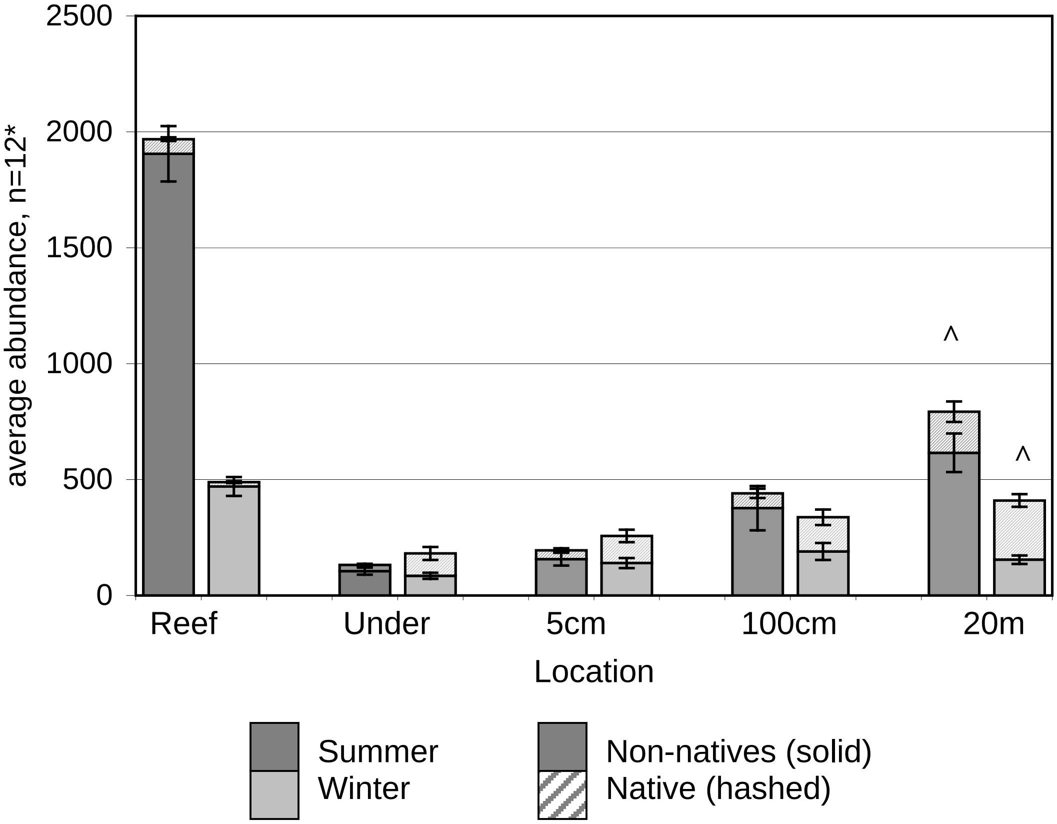


Fig. 3.3 nMDS ordination of all samples. Reef samples are in black, mudflat samples adjacent to reefs in dark gray, and mudflat samples not adjacent to reefs are in light gray.

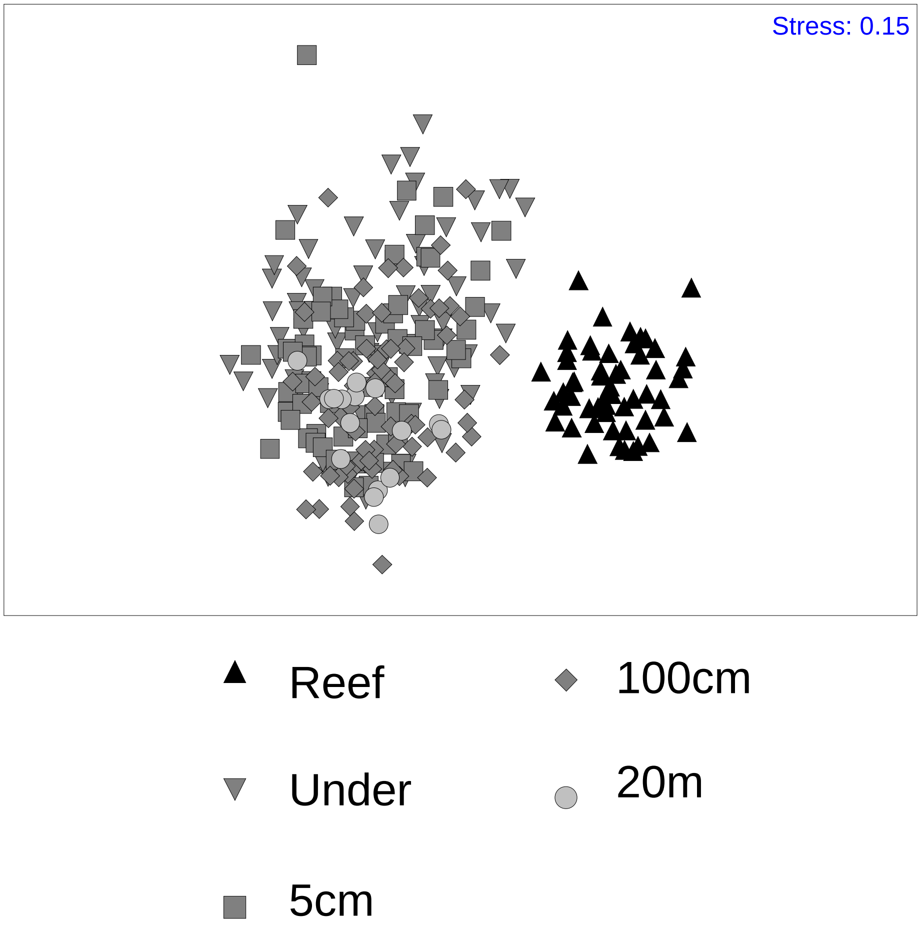


Fig. 3.4 Total abundance of infauna in mudflat samples from specific locations and experimental treatment groups. a) Summer before samples. b) Summer samples taken 6 months after experimental manipulation. c) Summer samples taken 1 year after experimental manipulation. d) Winter before samples. e) Winter samples taken 6 months after experimental manipulation. f) Winter samples taken 1 year after experimental manipulation. The date for each sampling period is listed above the graphs.

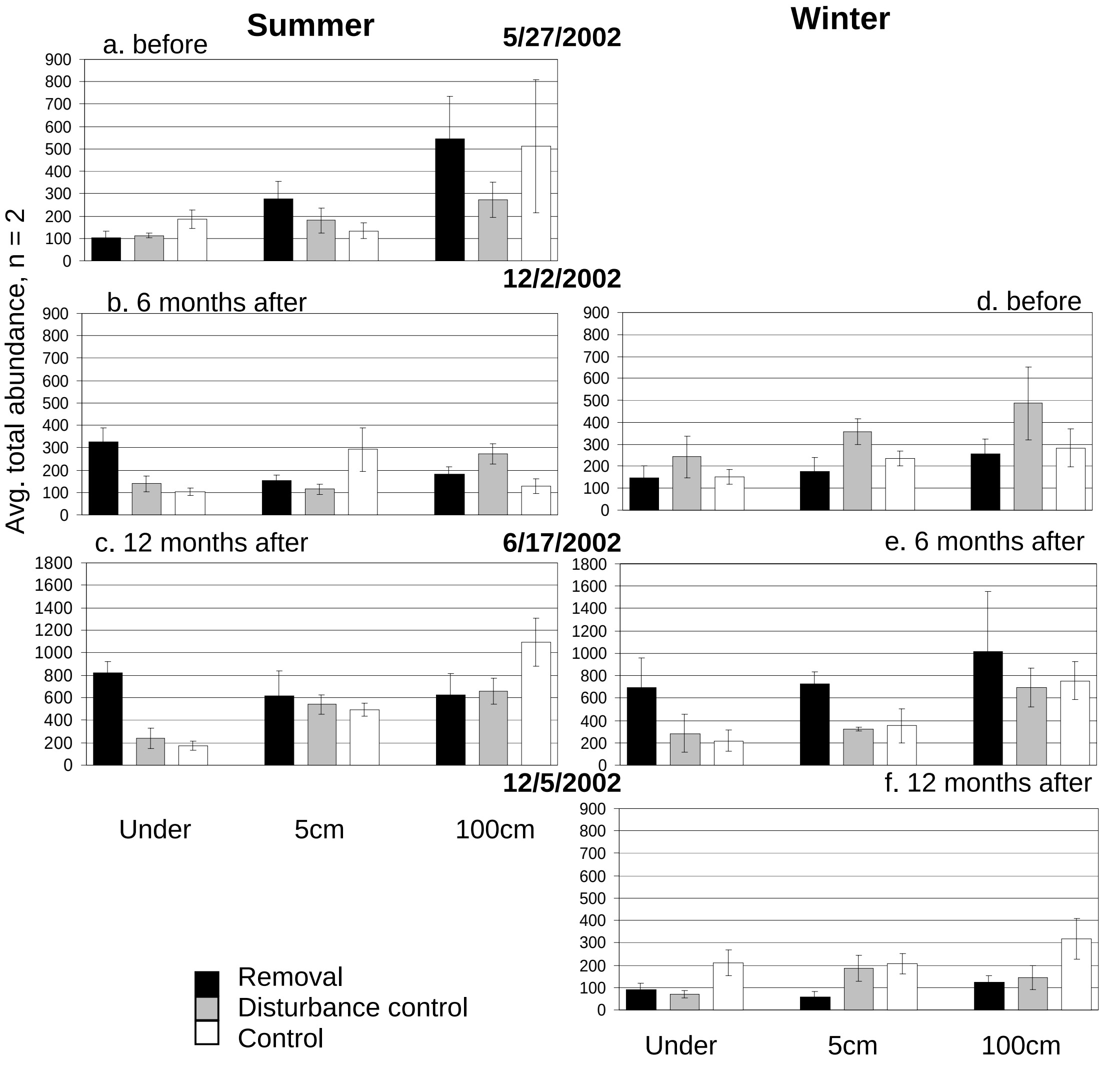


Fig. 3.5 *R*-values from ANOSIM analysis of square root transformed Bray-Curtis dissimilarities of treatment group pairs at specified times post experimental manipulation. a) Summer samples, b) winter samples. * Significant *R*-values.

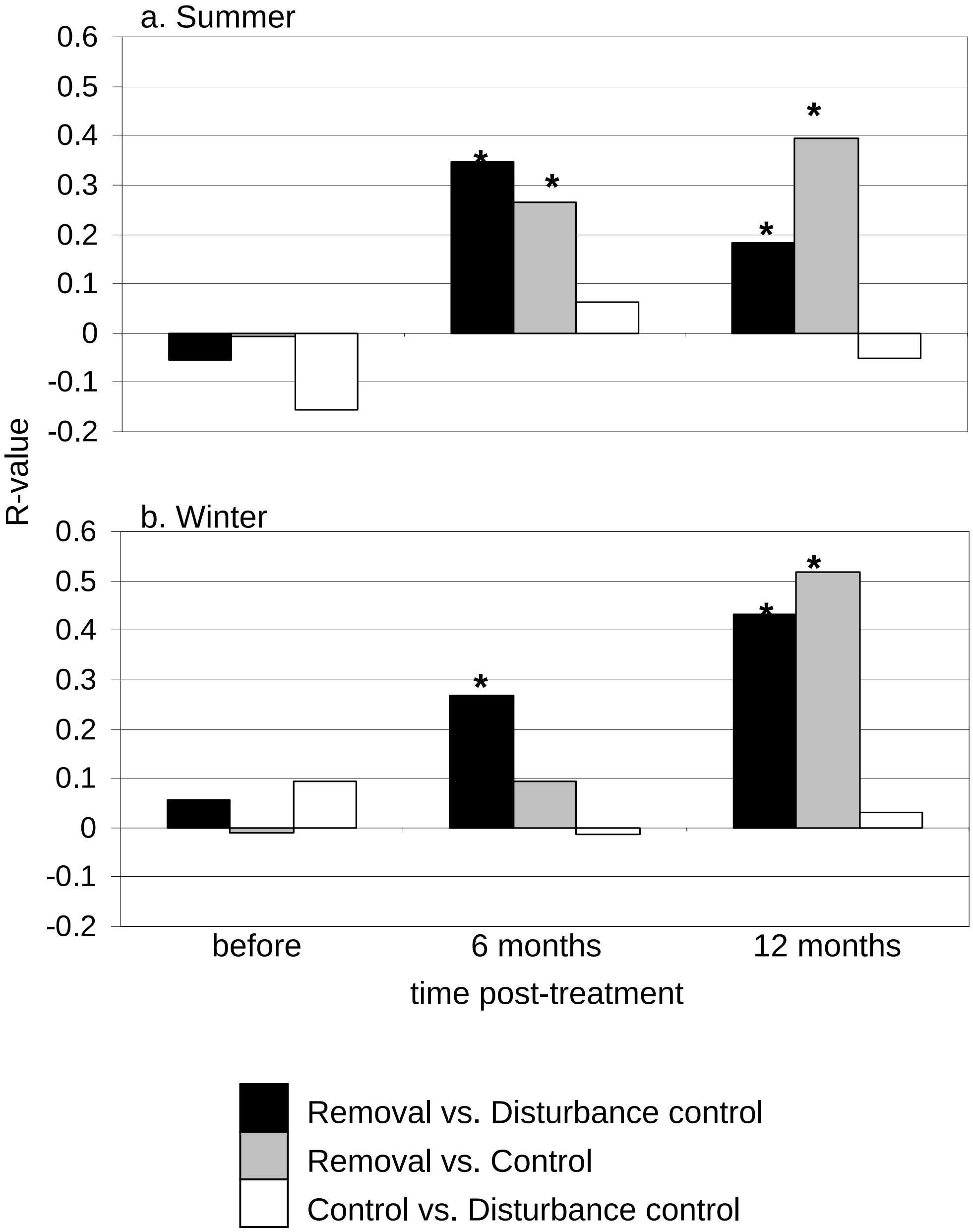


Fig. 3.6 Species richness (calculated by classical ACE estimation) per reef unit (reef samples plus nearby mudflat samples under, 5 cm, and 100 cm away from reefs) as a function of treatment group and time post experimental removal.

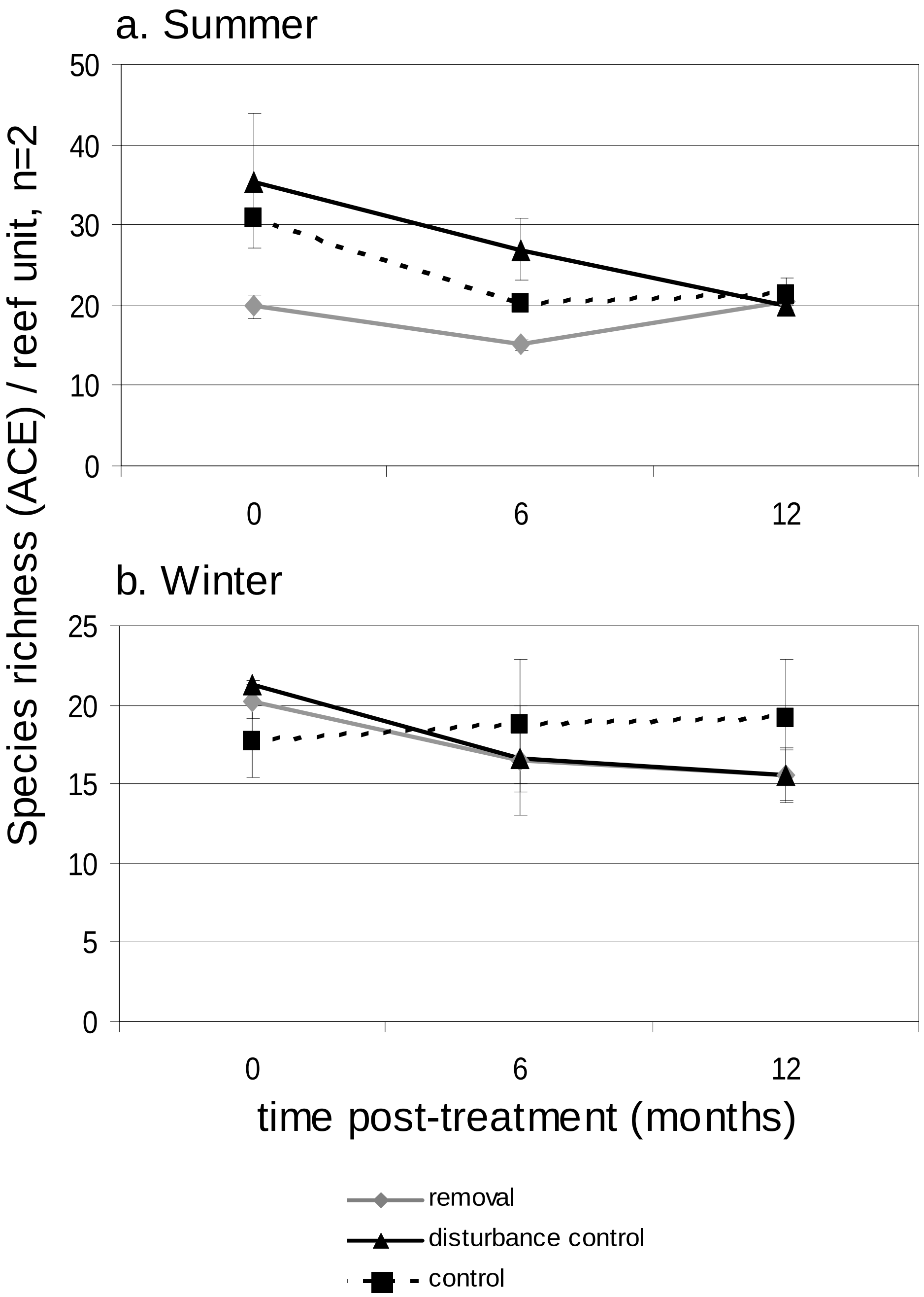


Fig. 3.7 Sediment grain size for specified treatments at specified sampling locations. a) Sands before experimental manipulation, b) fines before experimental manipulation, c) sands 1 year after experimental manipulation, d) fines 1 year after experimental manipulation. n = 2 for each bar.

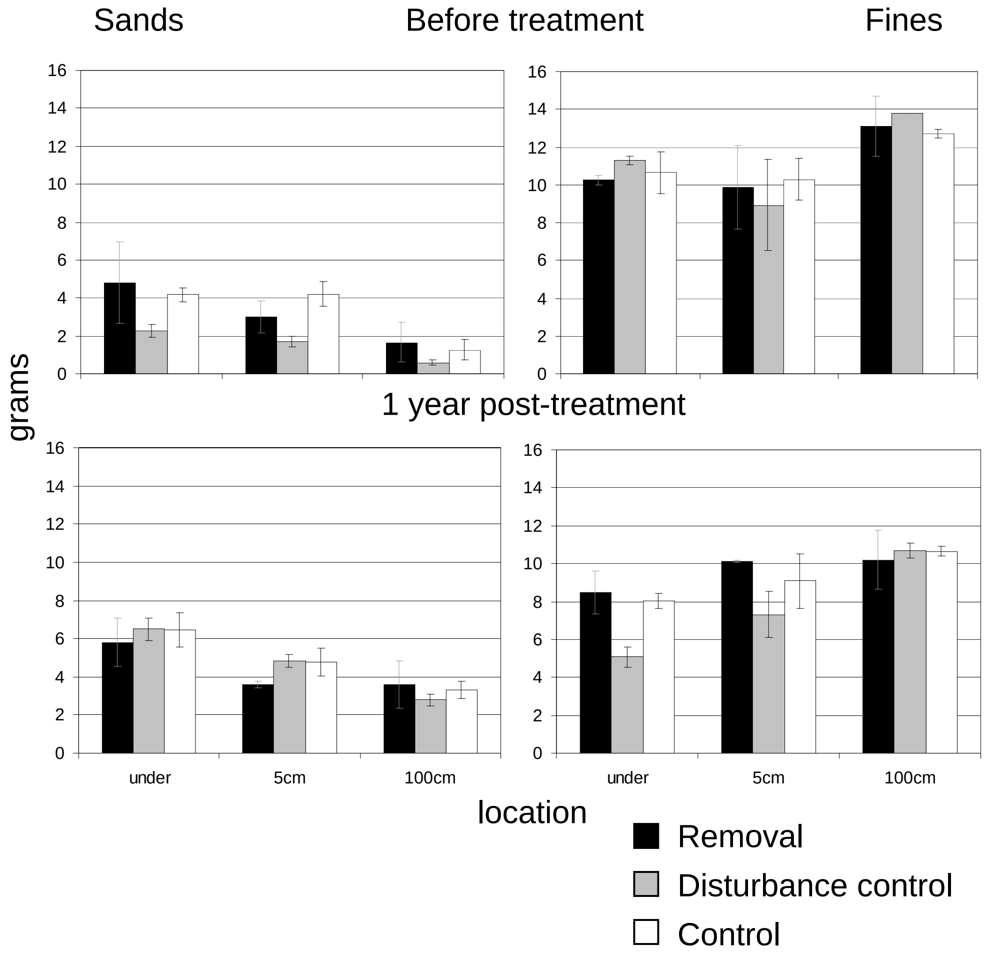


Fig. 3.8 Percent organics in sediment samples from different experimental treatment groups before and 1 year after treatment. a) Summer, b) winter.

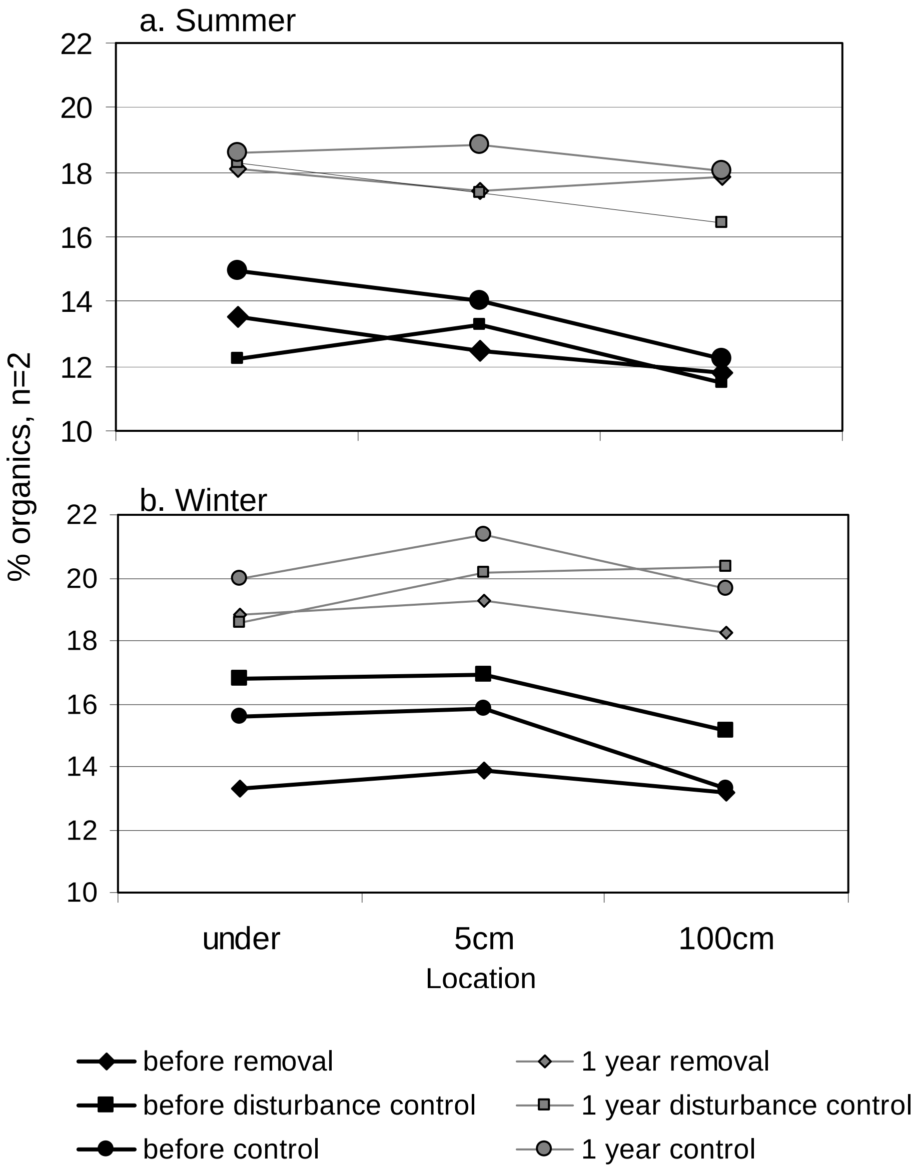
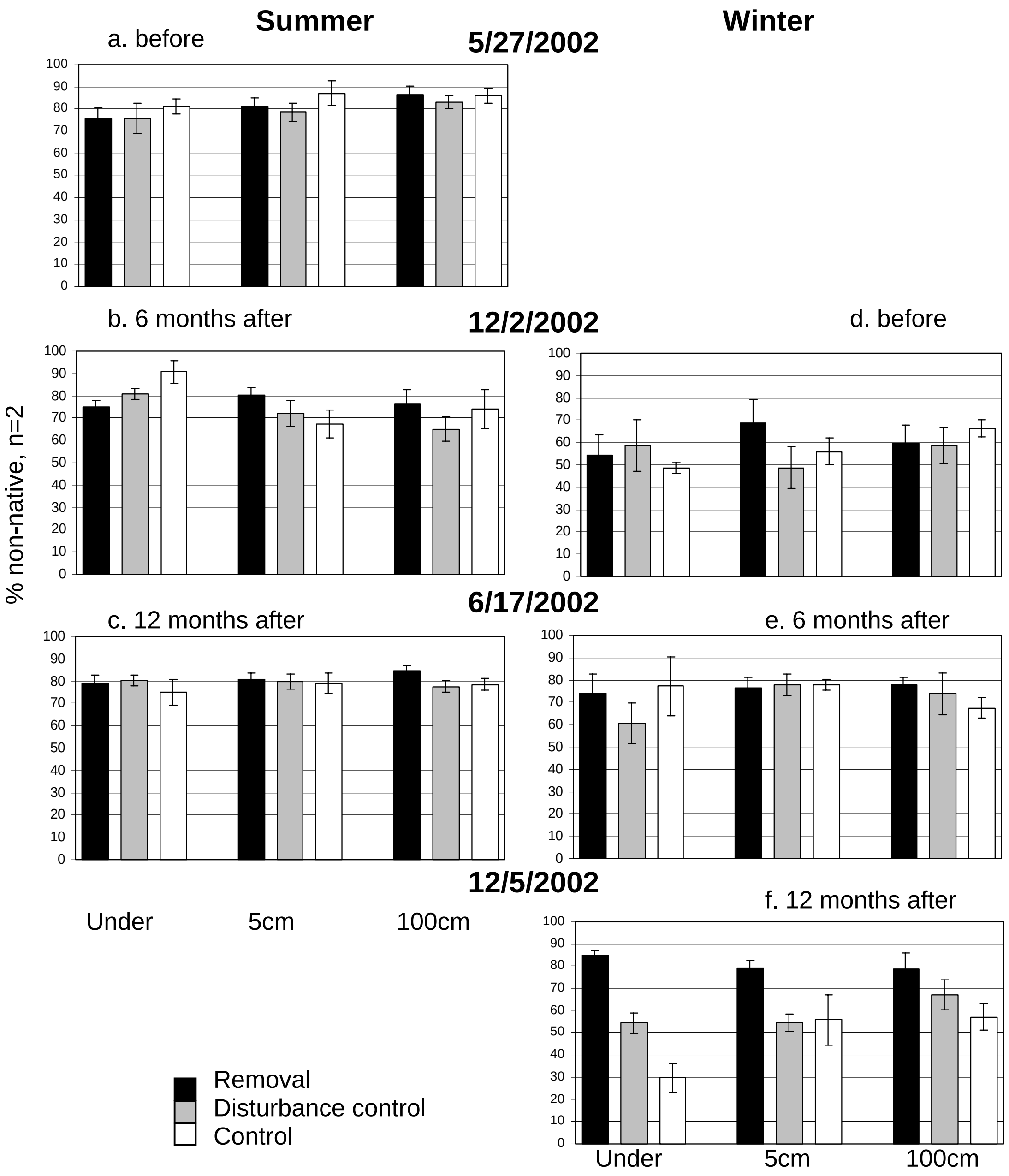


Fig. 3.9 Percent non-native species in mudflat samples from specific locations and experimental treatment groups. a) Summer before samples. b) Summer samples taken 6 months after experimental manipulation. c) Summer samples taken 1 year after experimental manipulation. d) Winter before samples. e) Winter samples taken 6 months after experimental manipulation. f) Winter samples taken 1 year after experimental manipulation. The date for each sampling period is listed above the graphs.



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-CHAPTER FOUR-

Invasional meltdown in non-native reefs: Comparing communities associated with invasive *Ficopomatus enigmaticus* and native *Ostrea conchaphila*

Coauthors: Nicholas Vidargas and Fiorenza Micheli

ABSTRACT

Introduction vectors for marine non-native species, such as oyster culture and boat fouling, often select for organisms dependent on hard substrates during some or all life stages. In prevalently soft-sediment estuaries, hard substrate may be a limited resource, which is increased through the introduction of habitat-creating non-native species. Positive interactions between non-native habitat-creating species and non-native species that utilize that habitat could be a mechanism for enhanced invasion success. Most previous studies on aquatic invasive habitat-creating species have demonstrated positive responses in associated communities, but few have directly addressed impacts on other non-native species. We examined the effect of an invasive habitat-creating species on associated native and non-native species by comparing communities associated with non-native reef-building tubeworms *Ficopomatus enigmaticus* and native oysters *Ostrea conchaphila* in Elkhorn Slough, a central California estuary. Non-native habitat supported greater densities of associated organisms – primarily highly abundant non-native amphipods (e.g. *Monocorophium insidiosum*, *Melita nitida*) and tube-dwelling polychaetes (*Sinelobus stanfordi*, *Polydora* spp.). Detritivores were the most common trophic group, making up disproportionately more of the community associated with *F. enigmaticus* than *O. conchaphila.* Analysis of similarity (ANOSIM) showed native species' community structure varied significantly among locations, but not between biogenic habitats. In contrast, non-natives varied with biogenic habitat type but not location. Thus, presence of *F. enigmaticus* reefs appears to enhance local non-native abundances, indicating facilitation by this habitat-creating non-native.

INTRODUCTION

Invasive species are a major threat to terrestrial and an increasing threat to marine biodiversity (Wilcove et al. 1998, Kappel 2005). Invasive species are organisms that have been transported by humans into a region not previously occupied, have established, and are causing or likely to cause economic or environmental harm (Carlton 2001). Non-native species are defined as those that fit the above definition but without known detrimental impacts. One of the key factors affecting the establishment and subsequent population growth of non-native species is the presence of necessary resources (such as food, living space, and light for photosynthetic organisms) in their recipient environment. An increase in the availability or accessibility of limited resources is likely to have a negative effect on a habitat's resistance to non-native species establishment (Davis et al. 2000, Davis & Pelsor 2001). Davis's hypothesis is based on the assumption that non-native species need certain resources and that their establishment success will be enhanced if they gain access to these resources without having to compete with resident species (Davis et al. 2000). Resource availability can be enhanced by a decrease in the resident community's use of the resource or by an increase in the resource supply.

Several major marine transport and introduction vectors select for organisms that utilize hard substrates (e.g. boat fouling, rock ballast, and aquaculture of bivalves such as oysters (Carlton 1996, Wonham & Carlton 2005)). Many of the most heavily invaded marine ecosystems (bays, estuaries, lagoons, and ocean inlets) were historically soft-sediment environments with limited amounts of naturally occurring hard substrates. Thus, suitable hard substrates in the recipient estuarine environments may be a limiting resource for non-native species. The abundance of hard substrates within these invaded marine ecosystems has increased and will likely continue to increase through anthropogenic structural additions associated with the construction of seawalls, harbors, docks, and bridges in these typically densely populated coastal areas. An additional mechanism of hard substrate addition is through the introduction of non-native species that themselves create habitat (for example bivalves, tubeworms, and submerged and marsh vegetation). Positive interactions with non-native habitat-forming species may enhance the establishment and population growth of other non-native species that utilize the new habitat. This process is an example of an “invasional meltdown,” in which non-native species facilitate ongoing and subsequent invasions by increasing the likelihood of survival, population size, and magnitude or extent of ecological impacts of other non-native species (Simberloff and Von Holle 1999).

Species that create habitats are most commonly referred to as “foundation species” (Dayton 1972, Ellison et al. 2005) or “ecosystem engineers” (Jones et al. 1994, 1997) and are defined as species that structure communities by creating locally stable conditions for other species and by modulating and stabilizing fundamental ecosystem processes (Ellison et al. 2005). These species are critical components of and defining organisms in a wide range of ecosystems, for example terrestrial temperate and tropical forests, coral reefs, and kelp forests. However, when non-native species invade an ecosystem and create new structural habitats there can be implications for community composition and fundamental ecosystem processes such as nutrient cycling, resource availability, and resilience to disturbances (references in Table 4.1).

In this study, we focus on benthic invertebrate communities that utilize native and non-native biogenic estuarine habitats. The identity, diversity, abundance, trophic mode, and microhabitat use of these small-bodied organisms are important to nutrient cycling, benthic-pelagic coupling, and food availability to organisms at higher trophic levels. Many different invasive phyla can provide structural habitat, from bivalves (*Dreissena* spp. and *Musculista senhousia*), submerged vegetation (*Caulerpa taxifolia*), marsh grasses (*Spartina* spp. and *Phragmites australis*), to tubeworms (*Ficopomatus enigmaticus* and *Sabella spallanzanii*), and tunicates (*Pyura praeputialis*). Table 4.1 provides a sampling of studies that have addressed the effects of some well-studied invasive aquatic ecosystem engineers on associated communities. The studies summarized in Table 4.1 show that most multi-species or community responses are either positive or a mix of positive and negative with only marsh plants, which simultaneously displace native plants and greatly reduce the quality and availability of mud habitat for infaunal species, having overall negative effects. One common impact of many invasive ecosystem engineers was an increase in the entrapment of fine sediments and the accumulation of pseudofeces resulting in associated communities dominated by detritivores as opposed to surface-feeding herbivores or suspension feeders, which tend to dominate un-invaded habitats (Stewart & Haynes 1994, Crooks & Khim 1999, Neira et al. 2005, Levin et al. *in press*). Results of this survey do not appear to be influenced by the research approach used; experimental manipulations as well as comparisons to native environments, with and without native ecosystem engineers, resulted in the generalized responses described above. Only two of the studies examined the effects of invasive habitat on associated non-native species, one showing a single species increase in abundance (Stewart et al. 1998) and the other a mix of positive and negative responses varying with species and location (Balata et al. 2004). This could be due to a lack of associated non-native species or because the authors did not ask this specific question. In either case, the question of whether non-native biogenic habitat can facilitate invasion and lead to invasional meltdown is largely unanswered.

In this study, we asked whether habitat provision by the invasive ecosystem engineer, *F. enigmaticus,* alters community structure and could provide a mechanism for invasional meltdown. We compared communities associated with the non-native reef-building serpulid polychaete, *F. enigmaticus*, to those associated with the native oyster, *Ostrea conchaphila*, in the central Californian estuary, Elkhorn Slough. Specifically, we examined differences in trophic groups' and non-native species' utilization of these habitats. A greater density or abundance of non-native species in the non-native reef habitat versus native habitat may indicate positive interactions between the non-native ecosystem engineer and associated non-native species and provide support for our hypothesis that habitat provision is a mechanism for invasional meltdown.

METHODS

Study system

Elkhorn Slough, a central Californian estuary (36º48.6 N, 121º47.1 W) 150 km south of San Francisco Bay, is a primarily soft-sediment environment composed of mid and low intertidal mudflats and high intertidal pickleweed *Salicornia virginica* zone. Opening of Elkhorn Slough's mouth and restoration of flow to previously diked wetlands have greatly enhanced erosion throughout the system, with the greatest impact in the system's main channels. Subtidal banks drop nearly vertically to an unstable shell bed bottom, which shifts with each tide change. Although the subtidal has hard substrates they are generally too unstable to provide suitable habitat for fouling organisms and will not be considered in this study (Heiman, personal observation).

There is evidence that the native oyster, *Ostrea conchaphila*, was abundant in the slough in the 1930s (MacGinitie 1935), however, oysters are currently found in low densities in clumps or as isolated individuals attached to hard surfaces in the intertidal (Hornberger 1991, Heiman, unpublished data). There is only one documented intertidal oyster reef (defined as covering 0.5 m^2 of the bottom), which covers approximately 7 m^2 and rises 10 -15 cm off the substrate (site F, Fig. 4.1a). This reef comprises a loose shell matrix only three layers thick, with live oysters only in the top layer. Oysters in Elkhorn Slough have an average maximum shell length of 5 cm and reach maximum densities of 340 oysters / m^2 in the reef described above (Heiman, unpublished data).

The only other major intertidal biogenic hard substrate found in this estuary is the reef-building non-native serpulid polychaete *Ficopomatus enigmaticus*, first observed in Elkhorn Slough in 1994 (Wasson et al. 2001). *F. enigmaticus* individuals live in calcareous tubes averaging 1.5 mm in diameter and 90 mm in length that are intertwined and cemented to each other forming masses up to 1 m tall and 5 m diameter (Heiman, unpublished data). Live worms are found primarily in the top 15 cm of reef matrix with densities reaching 60,000 individuals / m^2 (Heiman, unpublished data, Fig. 4.1b). Below this living layer, the reef is filled with mud.

In addition to *F. enigmaticus,* 57 marine non-native species have been reported for Elkhorn Slough (Wasson et al. 2001, Wasson et al. 2005). Most were introduced through fouling of small boats traveling from San Francisco Bay or with the aquaculture of Pacific (*Crassostrea gigas*) and eastern (*Crassostrea virginica*) oysters between the 1920s - 1980s. Oyster spat shipments from Japan and the Atlantic may have led to the introduction of 38 of the 58 non-native species (Gordon 1996, Wasson et al. 2001). Non-native oyster beds where once located throughout much of the slough, but are now absent due to collapse of the industry and the non-native oysters' inability to reproduce in cold Californian waters (Gordon 1996, Wasson et al. 2001).

Field sampling

To compare how native and non-native biogenic habitats are utilized by benthic invertebrates and whether they host different densities of non-native species, we sampled invertebrate communities associated with *F. enigmaticus* and native oysters. We took cores from biogenic habitat created by *F. enigmaticus* and/or *O. conchaphila* at six intertidal locations all between 20 to -20 cm MLLW between May and July of 2003 (Fig. 4.1). Both *O. conchaphila* and *F. enigmaticus* were found at two of the six sites (sites C and E, Fig. 4.1); only one habitat type was present at each of the other four sites. Sites spanned the distribution of oysters and *F. enigmaticus* in Elkhorn Slough. Three to ten cores (10 cm diameter) through the biogenic habitat (from the surface of the reef or clump to the underlying substrate, 10 to 40 cm deep) were collected at each site. The number of cores sampled depended on the extent of biogenic habitat at a given site. Samples were sieved through 500 µm mesh in the field then preserved. All associated organisms were identified to species and counted under a dissecting microscope. To account for differences in sample volume, we standardized abundance data by two different metrics: water displacement volume and weight of each sample's biogenic hard substrate. We conducted all subsequent analyses using both metrics to see if standardization method affected the results. The patterns and significance levels were nearly identical regardless of standardization metric. Here, we present the results for the weight-standardized data.

Statistical analysis

Community composition of associated fauna was compared between habitat types (*O. conchaphila* or *F. enigmaticus*), among locations within Elkhorn Slough (sites A – F, Fig. 4.1), and between patch sizes within each biogenic habitat type (reef = biogenic habitat covering at least 0.5 m^2 of the bottom, found at sites A for *F. enigmaticus*, and E for *O. conchaphila*; clump = surface area less than 0.5 m^2, at sites B, C, E for *F. enigmaticus* and C, D, F for *O. conchaphila*) using multivariate analyses conducted with PRIMER v. 5 (PRIMER-E Ltd, Plymouth, UK). Bray-Curtis dissimilarity (Bray & Curtis 1957) between pairs of samples was calculated on square-root transformed abundances to downweight the effect of the most common species on community dissimilarity. Patterns of dissimilarity among samples were visualized using non-metric Multidimensional Scaling (nMDS) ordinations. We conducted 1-way analysis of similarity (ANOSIM) on samples from *F. enigmaticus* and *O. conchaphila* separately to test if communities associated with a specific biogenic habitat varied with habitat size (i.e. reefs vs. clumps). We tested for significant differences in community structure between habitat types and among locations using 2-way crossed ANOSIMs on samples from the two locations with both habitat types (sites C and E, Fig. 4.1) as well as the whole dataset including all sites and samples. The taxa driving observed differences between groups of samples were identified using similarity percentage (SIMPER) analyses. Dunn-Šidák corrections were used to adjust significance levels to account for multiple tests (Sokal & Rohlf 1995).

In addition to conducting analyses on all taxa, we examined patterns for native and non-native species separately. Species were classified as native to Elkhorn Slough, non-native, or cryptogenic (species of unknown origin, (Carlton 1996)) based on the following references: Carlton 1979, Morris et al. 1980, Ruiz et al. 2000, and Wasson et al. 2001. 2-way ANOSIMs (location × habitat type) on first the non-native then the native components of the community were conducted for the two sites with both biogenic habitats as well as for the entire dataset. Cryptogenic species (which accounted for only 0.7 % of the total organisms in this study) were omitted from the above analysis.

Trophic groups are related to ecosystem-level functions, such as the transfer of primary productivity through benthic foodwebs, and may be indicators of habitat characteristics such as food availability (Whitlatch 1980, Pearson 2001). We pooled species into trophic groups to examine variation in the feeding biology of species associated with native and non-native habitats. Species' abundance data were pooled into the following trophic groups: carnivores, detritivores, herbivores, omnivores, and suspension feeders. Some infaunal taxa with flexible feeding strategies can be categorized into more than one trophic group (Levinton 1991). When this occurred, the species' abundance was divided evenly between the trophic groups (Bonsdorff & Pearson 1999). Only two polychaete species (*Polydora ligni* and *Polydora socialis*, accounting for 0.4 % of the organisms in this study) had flexible feeding strategies switching between suspension feeding and surface detritivory with changes in flow speed (Fauchald & Jumars 1979).

RESULTS

Thirty species were identified in benthic cores from different locations and habitat types: 18 natives, 10 non-natives, and 2 cryptogenic species (Table 4.2). Seven species (5 natives, 2 non-natives) were found only in association with *Ficopomatus enigmaticus*, and 4 species (3 natives, 1 non-native) were found only in association with *Ostrea conchaphila* (Table 4.2). All species except the oligochaetes *Tubificoides brownae* and *Thalassodrilides gurwitschi* were denser in the *F. enigmaticus* habitat than oyster habitat (average density / 100 g of biogenic habitat, *T. brownae*: oyster = 3.09 / 100 g, *F. enigmaticus* = 2.69 / 100 g; *T. gurwitschi*: oyster = 2.83 / 100 g, *F. enigmaticus* = 1.65 / 100 g).

Thirteen of the thirty species in this study were detritivores, including the numerically abundant amphipod *Monocorophium insidiosum*, tanaid *Sinelobus stanfordi*, and polychaete *Cirritulus cirratus*, making detritivores the most abundant (79 % of all organisms) and taxonomically diverse trophic group in this study. Omnivores were the second most taxonomically diverse trophic group with 6 species. However, omnivores made up only 3.6% of the organisms in this study. There were only four herbivorous species, including the abundant amphipod *Melita nitida*, with this group comprising 16.6% of our study's organisms. There were five carnivorous species, which accounted for 0.3% of all organisms in this study. Suspension feeders were also infrequently found (0.8% of organisms) and included only four species, two *Polydoria* spp. which can switch to detritivory in slower flow.

The structure of associated communities varied significantly with patch size in *F. enigmaticus* habitat (reefs vs. clumps, 1-way ANOSIM, $R = 0.721$, $p = 0.001$), but not for *Ostrea conchaphila* habitat (1-way ANOSIM, $R = 0.041$, $p = 0.337$). Differences between communities from *F. enigmaticus* reefs and clumps were driven by significantly higher densities of two non-native species in clumps, *M. insidiosum* (average abundance in reefs = 165.87 / 100 g of biogenic habitat, clumps = 503.10 / 100 g; ANOVA $F = 5.60$, *df* 1 & 18, $p = 0.0294$) and *S. stanfordi* (average abundance in reefs = 0.56 / 100 g of biogenic habitat, clumps = 50.26 / 100 g; ANOVA *F* = 95.66, *df* 1 & 18, *p* = 0.00001). In addition, samples collected from the center of *F. enigmaticus* reefs contained significantly lower densities of associated organisms compared to samples from the edge of reefs (average abundance in reef interior = 32.73 / 100 g, reef edge = 411.67 / 100 g; ANOVA *F* = 40.79, *df* 1 & 8, *p* = 0.0002).

ANOSIM produces a test statistic, *R*, which compares the average rank dissimilarity within and between groups of samples and can be compared across different ANOSIM analysis (Clarke & Warwick 1994). The greater the *R*-value for a particular factor (e.g. habitat type), the greater the similarity of samples within a habitat type versus between habitat types (i.e., the more variance in community structure is explained by that particular factor, in this case habitat type). At the two sites with both habitat types (sites C and E, Fig. 4.1), communities exhibited clear and significant separation between locations when all species were included in the analyses (2-way ANOSIM, *R* = 0.5, *p* = 0.002; Fig. 4.2a), with further clustering evident according to the type of biogenic habitat (*Ficopomatus* vs. *Ostrea*; 2-way ANOSIM, *R* = 0.567, *p* = 0.005, Fig. 4.2a). When only native species were considered, most of the variation in community structure appeared to be driven by differences between sampling locations (2-way ANOSIM, location: *R* = 0.591, *p* = 0.001; habitat type: *R* = 0.214, *p* = 0.024, non-significant after Dunn-Šidák correction; Fig. 4.2b). In contrast, most of the variation in community structure was associated with habitat type for non-native species (2-way ANOSIM, location: *R* = 0.414, *p* = 0.026, non-significant after Dunn-Šidák correction; habitat type: *R* = 0.645, *p* = 0.006; Fig. 4.2d) and for trophic groups (2-way ANOSIM, location: *R* = 0.322, *p* = 0.057; habitat type: *R* = 0.653, *p* = 0.004; Fig. 4.2c).

These patterns remained consistent regardless of whether we used the conservative analysis of only samples from the two sites with both biogenic habitat types (Fig. 4.3a, *R* and *p* values as reported above), or whether we expanded the analysis to include all samples from all sites (Fig. 4.3b, all *R* values are significant, except for location differences for trophic groups). When all locations and all species were included, biogenic habitat type and location explained similar amounts of the variation among samples (Fig. 4.3). More of the variation in native species' distributions was explained by location than habitat type, whereas the opposite was true for non-native species and trophic groups (Fig. 4.3).

Variation in communities between habitats was driven by differences in the abundances of five species: three highly abundant non-natives, the amphipods *M. insidiosum, M. nitida*, and the tanaid *S. stanfordi*, and two natives, the polychaete *C. cirratus* and the crab *Hemigrapsus oregonensis* (Table 4.3). The trophic groups driving community patterns were detritivores and omnivores (Table 4.3), respectively explaining 45.5 % and 25 % of the differences between the two different habitat types (Table 4.3). All of these species and trophic groups were more abundant in *F. enigmaticus* samples than in *O. conchaphila*, some as much as 16 times more abundant (Table 4.3). However, when relative proportion of the community associated with each habitat type was calculated for each species and trophic group, only the most abundant species and trophic group were more common (as a proportion of the total community) in *F. enigmaticus* habitats (Table 4.3).

DISCUSSION

Ficopomatus enigmaticus and *Ostrea conchaphila* occupy similar tidal elevations and provide hard structure in predominantly soft-sediment environments but support significantly different communities. Our study provides evidence for positive interactions between the non-native *F. enigmaticus* and other non-native species within Elkhorn Slough. Dense associations of non-native species were seen in the non-native *F. enigmaticus* habitat and not in the native oyster habitat. The numerically dominant non-native species in our study preferentially associated with the non-native habitat. In contrast, variation in the native component of associated communities was explained more by location than by biogenic habitat type. We suggest that the provision of habitat by *F. enigmaticus* is a mechanism for invasional meltdown within this estuary. The high abundance of non-natives may indicate a loss of resistance to invasions with the addition of *F. enigmaticus*, where non-native population persistence and growth may be facilitated by the availability of structural habitat. The high abundance of detritivores in both habitats, but especially within *F. enigmaticus* reefs, suggests that the communities of associated organisms rely on accumulation of organic matter within these habitats for food. Our study supports the findings outlined in Table 4.1: invasive biogenic habitats can have positive effects on associated communities, such as increasing species' densities. The communities associated with many of the non-native biogenic habitats examined in the studies in Table 4.1 are often dependent on an increase in organic matter due to pseudofeces accumulation, a mechanism which may be at work here as well.

Abundances of associated fauna may also be enhanced within *F. enigmaticus* because its complex, three-dimensional structure provides refugia from predation. Matsumasa (1994) found that the type of secondary substrate directly determined the identity of the most abundant associated crustaceans. Increases in associated fauna in experimental manipulations of the invasive bivalves *Musculista senhousia* and *Dreissena polymorpha* were also attributed to structural complexity of the biogenic habitats (Crooks & Khim 1999, Horvath et al. 1999). The complex structure of *F. enigmaticus* reefs, formed by the intertwining small calcareous tubes may explain why most of the species examined were more abundant in the invasive reefs than in the native oyster habitat, even after standardizing by sample weight or volume to account for differences in the amount of biogenic material. The availability of crevices as refuges for associated organisms may also explain the greater faunal abundances found at the edges compared to the centers of *F. enigmaticus* reefs, where crevices are filled with anoxic mud (Heiman, unpublished data). In contrast, the loose shell matrix throughout the oyster beds may explain the lack of community variation between the edges and center of the *O. conchaphila* reefs.

Location within Elkhorn Slough explained a greater proportion of the variation in the native component of reef-associated invertebrate communities than biogenic habitat type, whereas the opposite was true for non-native species. Many of the native species found in Elkhorn Slough evolved in soft-sediment habitats, where they likely developed adaptations to specific environmental conditions such as sediment grain size, salinity, and oxygen content of the sediments and water. Different locations within Elkhorn Slough support different sediment, salinity, and temperature conditions, potentially explaining why native communities exhibit significant between-site variation. Conversely, many non-native species have broad environmental tolerances for salinity (Ruiz et al. 2000), and possibly temperature and oxygen levels, allowing them to colonize opportunistically a broad range of locations. However, non-native species may have highly specific microhabitat preferences within these locations. For example *Monocorophium insidiosum*, a tube-dwelling amphipod, can tolerate wide salinity ranges (Kevrekidis 2004) but is often found in higher abundances on complex biogenic structures, even though it can exist in mudflats (Carlton 1979, Heiman, personal observations).

The suspension feeding *F. enigmaticus* likely plays an important role in the transfer of pelagic production to the benthos. The high abundance of detritivores within the non-native reefs may be the result of enhanced local availability of organic matter in the sediments through sediment entrapment and pseudofeces accumulation. Similar results have been observed in a number of other invasive marine ecosystem engineers such as the mussels *D. polymorpha* and *M. senhousia* (Stewart & Haynes 1994, Crooks & Khim 1999). These abundant associated species may or may not provide food resources for higher trophic groups depending on how much protection from predation the biogenic habitat provides. Fish and shrimp have been observed foraging above submerged *F. enigmaticus* reefs (Heiman, personal observations), suggesting that some predators can access either the associated communities or *F. enigmaticus* itself. Further foodweb studies are required to address this possibility.

There are multiple ways habitat forming non-native marine invertebrates can impact estuarine ecosystems. In this chapter, we have explored the role of non-native species in creating habitat for native and non-native benthic communities. Other ecosystem-level effects of an abundant suspension feeding invader like *Ficopomatus enigmaticus*, such as alteration of water clarity and effects on phytoplankton communities, may also be important (Davies et al. 1989). *F. enigmaticus* and other non-native species that form biogenic habitat, especially those that suspension feed, may constitute strongly interacting species in their new environments, with cascading effects on ecosystem structure and function (Heiman 2005, Soulé et al. 2005). Because *F. enigmaticus* has the potential to affect multiple ecosystem processes, it is a prime target for directed management efforts. Our results suggest that focusing research, control, and eradication efforts on strongly interacting invasive species such as *F. enigmaticus* may additionally result in the control of a suite of other non-native species and the prevention of further invasional meltdown.

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Table 4.1 Overview of aquatic invasive ecosystem engineers and their effects on associated communities. -/+ = negative and positive effects on different components of the community were observed either within the same study or in different studies. * n/m = not measured or addressed directly by the studies cited.

Phylum	Species	Geographic region	Habitat	Experimental manipulation	Compared to native biogenic habitat	Compared to uninvaded habitat without biogenic species	multi-species response	Non-native species response	References
Annelida	*Ficopomatus enigmaticus*	Argentina, England, Adriatic Sea	lagoon, river delta	no	no	yes	**+**	* n/m	Thomas & Thorp 1994, Bianchi & Morri 1996, Schwindt & Iribarne 2000
Annelida	*Sabella spallanzanii*	Southern Australia	hard substrate	yes	no	yes	Indeterminate	* n/m	Holloway & Keough 2002
Anthophyta	*Phragmites australis*	Atlantic USA	marsh	no	yes	no	**-**	* n/m	Posey et al. 2003, Silliman & Bertness 2004
Anthophyta	*Spartina alterniflora x S. foliosa hybrid*	San Francisco Bay, USA	marsh/ mudflat	no	yes	yes	**-**	* n/m	Neira et al. 2005, Brusati & Grosholz in press, Levin et al. in press
Anthophyta	*Zostera japonica*	Coos Bay, USA	seagrass bed/ mudflat	yes	no	yes	**+**	* n/m	Posey et al. 1988
Bryozoa	*Watersipora subtorquata*	Northern Australia	hard substrate	yes	yes	yes	**+**	* n/m	Floerl et al. 2004
Chlorophyta	*Caulerpa taxifolia*	French Mediterranean	shallow subtidal	yes	yes	yes	**-/+**	* n/m	Meinesz 1999 and references there in
Chlorophyta	*Caulerpa taxifolia / C. racemosa*	Mediterranean	shallow subtidal	no	no	yes	**-/+**	**-/+**	Piazzi et al. 2003, Balata et al 2004
Chromophycota	*Sargassum muticum*	Northern Spain	rocky coast	no	yes	no	none	* n/m	Viejo 1999
Mollusca	*Mytilus galloprovincialis*	South Africa, Southern Australia	lagoon, seawall	no	yes	yes	**-/+**	* n/m	Robinson & Griffith 2002, Chapman et al. 2005
Mollusca	*Dreissena polymorpha*	Great Lakes, USA	hard substrate	yes	no	yes	**-/+**	* n/m	Karatayev et al. 1997, Ricciardi et al. 1997, Horvath et al. 1999, Kuhns & Berg 1999
Mollusca	*Dreissena polymorpha / D. bugensis*	Great Lakes, USA	hard substrate	no	no	yes	**+**	**+**	Stewart & Haynes 1994, Stewart et al. 1998
Mollusca	*Musculista senhousia*	New Zealand, Pacific USA	mud/ sandflat	yes	no	yes	**-/+**	* n/m	Creese et al. 1997, Crooks & Khim 1999
Urochordata	*Pyura praeputialis*	Chile	rocky shore	no	no	yes	**+**	* n/m	Castilla et al. 2004

Table 4.2 List of all species associated with *Ficopmatus enigmaticus* reefs and/or *Ostrea conchaphila*. * Trophic group abbreviations: C = carnivore, D = detritivore, O = omnivore, H = herbivore, S = suspension feeder. **Invasion status abbreviations: N = native, I = introduced or non-native, C = cryptogenic. Introduction vector abbreviations: BW = ballast water, F = ship fouling, O = oysterculture, n/a = not applicable because species is native.

Phylum	Species	Trophic mode*	Invasion status**	Native geographic area	Introduction vector	Associated with *Ficopomatus*	Associated with *Ostrea*
Annelida	*Eteone californica*	C	N	East Pacific	n/a	X	X
Annelida	*Eumida bifoliata*	C	N	East Pacific	n/a	X	X
Annelida	*Halosydna brevisetosa*	C	N	East Pacific	n/a	X	
Annelida	*Boccardia hamata*	D	N	East Pacific	n/a	X	X
Annelida	*Boccardia proboscidea*	D	N	East Pacific	n/a	X	X
Annelida	*Capitella capitata*	D	C	cosmopolitan	F, O	X	X
Annelida	*Cirratulus cirratus*	D	N	cosmopolitan	n/a	X	X
Annelida	*Heteromastus filiformis*	D	I	amphi-Atlantic	BW, O	X	X
Annelida	*Streblospio benedicti*	D	I	West Atlantic	F, BW, O	X	X
Annelida	*Thalassodrilides gurwitschi*	D	N	East Pacific	n/a	X	X
Annelida	*Tubificoides brownae*	D	I	West Atlantic	BW, O	X	X
Annelida	*Polydora ligni*	D/S	I	West Atlantic	F, BW, O	X	
Annelida	*Polydora socialis*	D/S	N	East Pacific	n/a	X	X
Annelida	*Platynereis bicanaliculata*	G	N	East Pacific	n/a	X	
Arthropoda	*Carcinus maenas*	C	I	East Atlantic	BW		X
Arthropoda	*Phoxichilidium femoratum*	C	N	East Pacific	n/a	X	X
Arthropoda	*Cumella vulgaris*	D	N	East Pacific	n/a		X
Arthropoda	*Monocorophium insidiosum*	D	I	unknown	F, O	X	X
Arthropoda	*Sinelobus stanfordi*	D	I	unknown	F, BW	X	X
Arthropoda	*Allorchestes angusta*	H	N	East Pacific	n/a	X	
Arthropoda	*Grandidierella japonica*	H	I	West Pacific	F, BW, O	X	X
Arthropoda	*Melita nitida*	H	I	West Atlantic	F, BW, O	X	X
Arthropoda	*Elasmopus antennatus*	O	N	East Pacific	n/a		X
Arthropoda	*Hemigrapsis oregonensis*	O	N	East Pacific	n/a	X	X
Arthropoda	*Palaemon macrodactylus*	O	N	East Pacific	n/a	X	
Arthropoda	*Leptochelia dubia*	O	C	cosmopolitan	F	X	X
Arthropoda	*Pachygrapsis crassipes*	O	N	East Pacific	n/a	X	X
Arthropoda	*Nebalia gerkenae*	S	N	East Pacific	n/a	X	
Arthropoda	*Sphaeroma quoyanum*	S	I	West Pacific	F	X	
Mollusca	*Runcina macfarlandi*	H	N	East Pacific	n/a		X

Table 4.3 Species and trophic groups accounting for a majority of the variation between communities associated with *Ostrea conchaphila* and *Ficopomatus enigmaticus*. Results reported from SIMPER analysis of all samples across all sites. Numbers listed initially are average densities / 100 g biogenic habitat followed in brackets by the percent of the average community density represented by the listed species or trophic group. *Denotes non-native species.

Species	Avg. abundance in *Ficopomatus enigmaticus*	Avg. abundance in *Ostrea conchaphila*	Contribution to dissimilarity (%)
*Monocorophium insidiosum**	356.48 (65.7)	43.82 (33.8)	27.1
*Melita nitida**	89.57 (16.5)	5.37 (4.1)	14.8
*Sinelobus stanfordi**	28.64 (5.3)	2.67 (2.1)	8.0
Hemigrapsus oregonensis	12.63 (2.3)	0.77 (0.6)	6.9
Ciratulus cirratus	9.73 (1.8)	7.39 (5.7)	6.1
Trophic groups			
Detritivores	409.7 (82.7)	64.2 (51.7)	45.5
Omnivores	18.6 (3.8)	3.4 (2.7)	25.0
Herbivores	15.7 (2.9)	9.7 (8.1)	10.2
Suspension feeders	5.26 (1.1)	0.21 (0.2)	6.8

Fig. 4.1 Map of Elkhorn Slough, a central Californian estuary 150 km south of San Francisco Bay. Stars mark sites where *Ficopomatus enigmaticus* was sampled, circles where *Ostrea conchaphila* was sampled. Letters label sampling locations from north to south. a) The oyster reef at site E. b) The *F. enigmaticus* reef at site A. Scale bars on photos = 1 m.

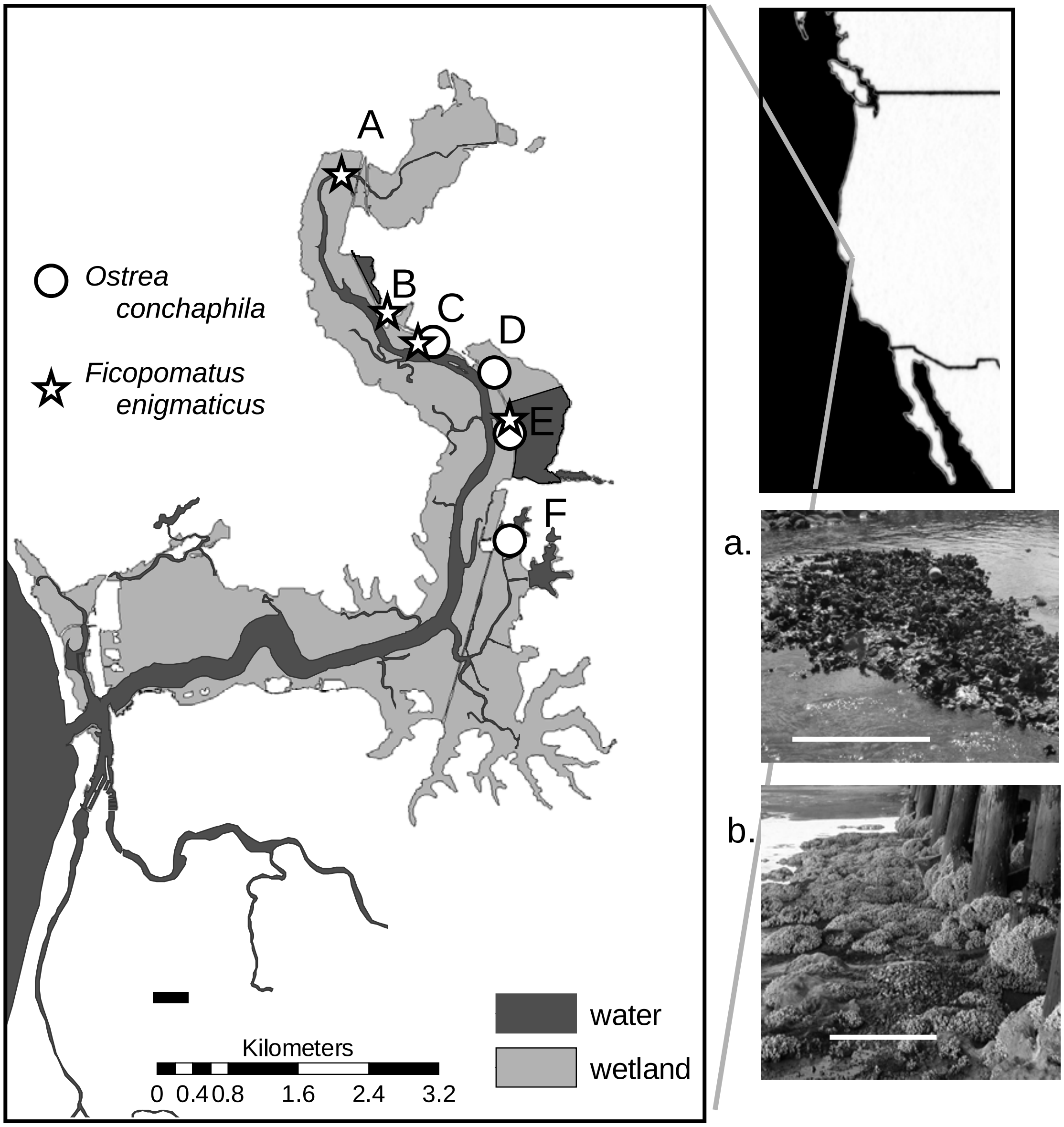


Fig. 4. 2 nMDS ordinations of infaunal community structure in samples from site C and E (the sites with both *Ficopomatus enigmaticus* and *Ostrea conchaphila* biogenic habitats) based on square root transformed Bray-Curtis dissimilarities. a) Bray-Curtis dissimilarities calculated with all species, b) with only native species, c) trophic groups, d) only non-native species.

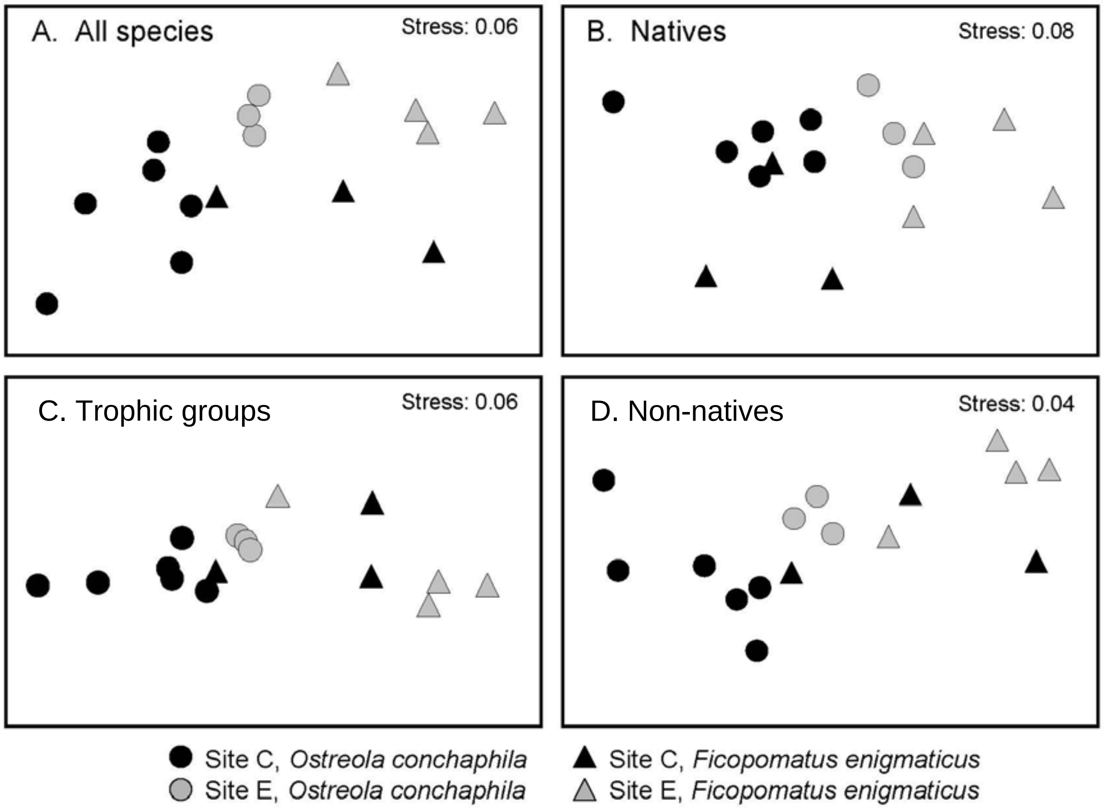
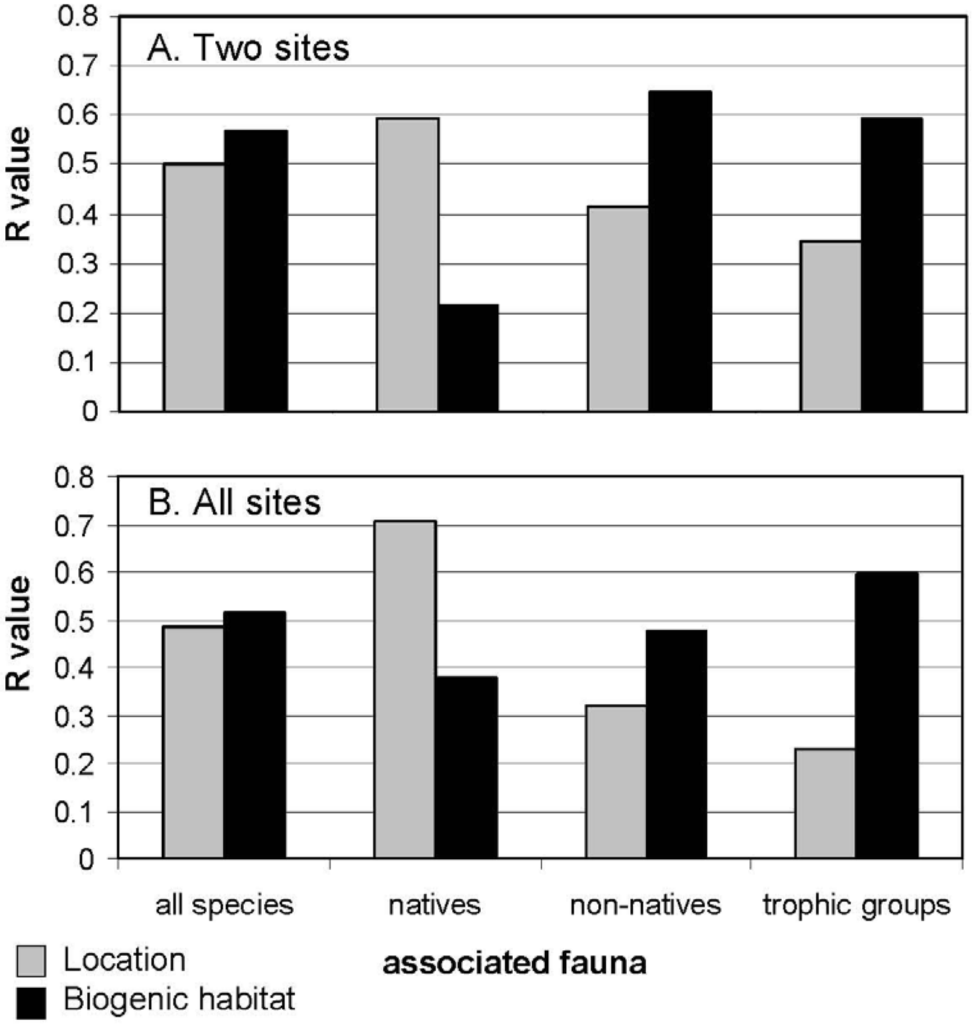


Fig. 4.3 Average dissimilarity between sites and biogenic habitats for infaunal community components: all species, only natives, only non-natives, trophic groups. *R*-values from ANOSIM analysis of square root transformed Bray-Curtis dissimilarities of specified community components in a) samples from sites C and E, b) all samples from all sites.



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