



## SYMPOSIUM

# Non-native Ecosystem Engineer Alters Estuarine Communities

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**Synopsis** Many ecosystems are created by the presence of ecosystem engineers that play an important role in determining species' abundance and species composition. Additionally, a mosaic environment of engineered and non-engineered habitats has been shown to increase biodiversity. Non-native ecosystem engineers can be introduced into environments that do not contain or have lost species that form biogenic habitat, resulting in dramatic impacts upon native communities. Yet, little is known about how non-native ecosystem engineers interact with natives and other non-natives already present in the environment, specifically whether non-native ecosystem engineers facilitate other non-natives, and whether they increase habitat heterogeneity and alter the diversity, abundance, and distribution of benthic species. Through sampling and experimental removal of reefs, we examine the effects of a non-native reef-building tubeworm, *Ficopomatus enigmaticus*, on community composition in the central Californian estuary, Elkhorn Slough. Tubeworm reefs host significantly greater abundances of many non-native polychaetes and amphipods, particularly the amphipods *Monocorophium insidiosum* and *Melita nitida*, compared to nearby mudflats. Infaunal assemblages under *F. enigmaticus* reefs and around reef's edges show very low abundance and taxonomic diversity. Once reefs are removed, the newly exposed mudflat is colonized by opportunistic non-native species, such as *M. insidiosum* and the polychaete *Streblospio benedicti*, making removal of reefs a questionable strategy for control. These results show that provision of habitat by a non-native ecosystem engineer may be a mechanism for invasional meltdown in Elkhorn Slough, and that reefs increase spatial heterogeneity in the abundance and composition of benthic communities.

## 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 assemblages 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 modification of the habitat by ecosystem engineers can also facilitate other organisms by increasing retention of propagules or the availability of limited resources (Eckman 1985). Positive interactions between ecosystem engineers and species that utilize the created habitat may be responsible for determining a habitat's species composition (Bruno and Bertness 2001).

Given the importance of ecosystem engineers for structuring local assemblages, how do assemblages respond to the introduction of a novel ecosystem engineer? Some non-native species have the ability to modify recipient environments to such an extent that they become new foundation species for these environments. For example, non-native cordgrass *Spartina* spp. in San Francisco Bay has turned extensive intertidal mudflats into marshes. These marshes host altered infaunal assemblages and have changed

geochemical processes (Neira et al. 2005; Brusati and Grosholz 2006; Levin et al. 2006). Abundant and dense root mats displace many infaunal organisms while the aboveground shoots decrease the availability of light to the sediments, thereby reducing benthic algal production and possibly explaining the shift from herbivores to below-ground detritivores (Levin et al. 2006). 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* (Stralberg et al. 2004). Similar dramatic ecological changes have been reported from other non-native ecosystem engineers such as the seagrass *Zostera japonica* (Posey 1988), the mussel *Musculista senhousia* (Crooks and Khim 1999), non-native earthworms (Holdsworth et al. 2007), and the non-native beaver, *Castor canadensis* (Anderson and Rosemond 2007).

While many studies have examined the effect of non-native marine ecosystem engineers on community structure, few have asked whether the addition of novel biogenic habitat by non-native species increases the abundance or diversity of other non-native species in the environment. The process of non-native species facilitating ongoing and subsequent invasions by increasing the likelihood of establishment, population growth, and magnitude or extent of ecological impacts of other non-native species is known as an invasional meltdown (Simberloff and Von Holle 1999). We hypothesize that non-native ecosystem engineers may facilitate other non-native species. Thus, invasion by non-native ecosystem engineers may represent a mechanism for invasional meltdown.

Due to common historical and modern vectors of the introduction of non-native species 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. By providing hard surfaces, non-native ecosystem engineers increase the availability of substrate which may be utilized by other non-native species. In this study, we examine the influences of a non-native ecosystem engineer on estuarine infaunal assemblages, and explore whether a non-native engineer enhances the abundance or diversity of other non-native species. We conducted experiments in a central Californian estuary where the reef-building tubeworm *Ficopomatus enigmaticus* has recently established.

Native to Australia, *F. enigmaticus* has invaded many locations around the world (e.g., Argentina, Japan, Hawaii, Europe), including the western coast of North America: most notably San Francisco Bay,

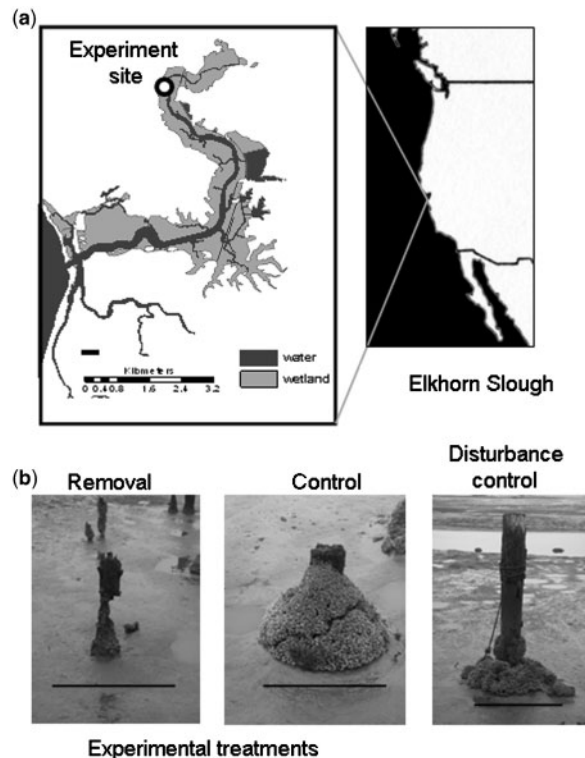
where it has persisted for over 90 years, and Elkhorn Slough, where it was first reported in 1994 (Carlton 1979; Wasson et al. 2001). *Ficopomatus enigmaticus* was probably introduced into San Francisco Bay and Elkhorn Slough through boat fouling (Carlton, 1979). In both locations, it has expanded rapidly, with large aggregations of calcareous tubes developing as the larvae gregariously settle on adult tubes. In Argentina, *F. enigmaticus* reefs have been shown to increase by nearly 10 cm in diameter each year (Schwindt et al. 2004).

*Ficopomatus enigmaticus* reefs can alter flow regimes and sedimentation rates, thereby modifying the physical environment and having direct and indirect effects on benthic assemblages (Schwindt 1998). Distinct assemblages have been recorded as associated with *F. enigmaticus* reefs throughout the world (Thomas and Thorp 1994; Bianchi and Morri 1996; Schwindt and Iribarne 2000; Schwindt 2001). In a previous study by Elkhorn Slough, *F. enigmaticus* reefs were shown to house distinctly different assemblages when compared to the only other hard biogenic habitat in the estuary, native oyster beds (*Ostrea lurida*) (Heiman et al. 2008). By providing a complex habitat in estuarine mudflats otherwise lacking hard substrate, *F. enigmaticus* reefs can have significant impacts on the physical environment, associated biota, and the interactions of species within invaded estuaries.

We conducted sampling and experimental removals of *F. enigmaticus* reefs to investigate their possible influences on the structure, diversity, and distribution of benthic invertebrate assemblages in Elkhorn Slough. Specifically, we addressed the following questions: (i) What species utilize the non-native habitat? Does *F. enigmaticus* act as a foundation species in its new environment? Is there evidence of an invasional meltdown occurring in this heavily invaded estuary following the establishment of non-native tubeworm reefs? (ii) Does *F. enigmaticus* alter the distribution and abundance of native and non-native infaunal assemblages in nearby mudflats?

## Methods

To determine what species associate with *F. enigmaticus* reefs and evaluate the effects of the reefs on nearby infaunal assemblages, we conducted a removal experiment in Elkhorn Slough, where extensive reefs are associated with wooden pilings (Fig. 1a). Each reef was ~1 m in diameter and 0.5 m tall, providing a set of over 100 replicated experimental units. We selected a subset of 12 reefs, located between -0.1 and 0.1 m MLLW for the experiment.



**Fig. 1** (a) Map of Elkhorn Slough with persistent waterways represented in dark gray and wetlands in light gray. (b) Pictures of reefs from different experimental treatment groups. Lines on photographs represent 1 m.

All experimental reefs and nearby mudflats were sampled before treatment, 6 months after treatment, and 1 year after treatment. To address possible seasonal differences in responses of the community to the experiment, treatments were initiated on two different dates: summer (May 27) and winter (December 2) 2002. Reefs were sampled by taking two 10 cm diameter clumps of the reef matrix from each reef. To account for differences in reef sample volume, we standardized associated infaunal abundance both by the volume of each clump, determined by water displacement, and by the weight of each sample. Since statistical results were identical for each standardization method we will report only weight-standardized results. To sample the mudflat community, two infaunal cores (10 cm diameter  $\times$  10 cm deep) were taken from the following locations: directly under the reef, after it was removed or sampled, 5 cm and 1 m away from the reef's edge. Additionally, to understand whether infaunal assemblages near the reef differed from assemblages not previously exposed to the reefs, eight infaunal cores (10 cm diameter  $\times$  10 cm deep) from a mudflat in the same general vicinity and tidal elevation, but at least 20 m from all *F. enigmaticus* reefs,

were collected 1-year after treatment for each sampling state date (see below). Cores and reef samples were sieved to 500  $\mu$ m mesh in the field, then cores and reef samples were preserved in a 10% formaldehyde solution for three days for fixation, after which the samples were transferred to 80% ethanol for storage. Samples were sorted under a dissecting microscope. All animals were identified to the lowest taxonomic group possible 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, J. T. Carlton, personal communication).

Following the initial infaunal and reef sampling, four reefs were completely removed, four remained unmanipulated to serve as controls, and four reefs were removed but then returned to their original location to evaluate the effects of experimental disturbance (Fig. 1b). For removal treatments, all reef material was scraped from the piling with a shovel, collected in large plastic tubs, and disposed of in the terrestrial environment. A boogie board, a styrofoam board with a curved front  $\sim$ 0.5 m by 1 m, was wedged under the disturbance-control reef before the reef was broken away from the piling. Careful prying with the shovel allowed large chunks of the reef to be broken off. The pieces of reef were then dragged at least 1 m away from the piling on the boogie board then carefully placed back around the piling. Two reefs in each treatment group (control, disturbance-control, and removal) were randomly assigned to the summer experiment and two were assigned to the winter experiment.

To assess the effects of non-native reefs on the benthic assemblages living in the nearby mudflats, we conducted univariate and multivariate analyses of the animal counts from infaunal cores. The total number of invertebrates present and the percent non-natives within infaunal cores were compared among experimental treatments and dates using nested analysis of variance (ANOVA) models with experimental treatment (removal, control, disturbance-control), season of removal (summer, winter), time of sampling (before removal, 6 months, and 1 year after removal), and location relative to reefs (under the reef, 5 cm away, and 100 cm away) as fixed factors. Reefs were a random factor nested within the treatment-by-season interaction. Dunn-Šidák corrections were used to adjust significance levels to account for two different ANOVA tests: (i) total invertebrate abundance and (ii) percent non-natives (Sokal and Rohlf 1995). To be

conservative, cyptogenic species were included as natives in this and all other relevant statistical tests.

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 one-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 reefs and mudflats, a one-way ANOSIM with location as the factor was conducted for all samples. Results of multivariate analyses are summarized by reporting *R*-values, which compare the average rank dissimilarity within and between groups of samples and can be compared across different ANOSIMs (Clarke and Warwick 1994). 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).

## Results

Thirty-one taxa were identified from the 137,746 organisms collected in this study. Thus, taxonomic diversity in benthic communities of the upper portion of Elkhorn Slough is low in reefs (24 taxa identified) and mudflats (30 taxa identified) (Table 1). Polychaetes, oligochaetes, amphipods, and isopods collectively comprised a majority of organisms identified in both habitat types (Table 1). Larger macroinvertebrates, including the native crab *Hemigrapsus oregonensis* and the non-native snail *Batillaria attramentaria*, were found in both reef and mudflat samples (Table 1). The assemblages within the reefs and in the mudflats near and far from reefs contained high abundances of non-natives (108,074 non-native organisms total), with an average of 78.5% non-natives (standard deviation = 18.1%) across all samples. The proportion of non-native organisms was greater in reef samples (average of 95.5%, standard deviation = 3.2%) as compared to mudflat samples taken from any distance from the *F. enigmaticus* reefs (average of 67.1%, standard deviation = 17%) (Fig. 2). Most of the taxa were found in both habitats but exhibited greater abundances in either the mudflat or the reef. Only a few rare taxa were found exclusively in only one environment (Table 1). Even

with the relative lack of habitat specificity observed in the taxa from this study, the assemblages living in the reefs had a significantly different composition than did assemblages found in any of the locations in mudflats (one-way ANOSIM global  $R=0.432$ ,  $P=0.001$ ). The differences in assemblage composition were driven by the highly abundant non-native amphipods *Monocorophium insidiosum* and *Melita nitida* in the reefs and the abundant non-native polychaete *Streblospio benedicti* and cryptogenic oligochaete *Thalassodrilides gurwitschi* in the mudflats.

*Ficopomatus enigmaticus* reefs affected total faunal abundance in nearby mudflats (Table 2 and Fig. 3). Effects varied with sampling date and season (ANOVA: season  $\times$  time  $\times$  treatment interaction  $F=5.5$ ,  $df=4$  and  $12$ ,  $P=0.0094$ ) (Table 2). There was an increase in infauna in the mudflats exposed by reef removal, primarily due to an increase in the abundance of *S. benedicti*, *M. insidiosum*, and *T. gurwitschi* (Fig. 3b, c, and e). This is particularly apparent when removals were conducted in the summer. Reefs also appear to depress faunal abundances in sediments underneath reefs and near their edges, compared to locations 1 m or more away from reefs (distance:  $P=0.0004$ , Table 2). Both before and after removals, there is a trend for more abundant infauna in samples 100 cm (Figs 2 and 3) and 20 m (Fig. 2) away from reefs compared to samples taken close to reefs.

Reef removals also had significant effects on assemblage structure in nearby mudflats. 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. 4a), although not in the winter experiment ( $R=0.094$ ,  $P=0.189$ ; Fig. 4b), and significantly different from disturbance-controls both in summer and winter treatments (summer  $R=0.347$ ,  $P=0.005$ ; winter  $R=0.267$ ,  $P=0.035$ ; Fig. 4a and b). These observed responses of assemblages persist through time, with the assemblages from where reefs were removed still being different both from disturbance-controls and from 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. 4a and b). These patterns of responses by assemblages are determined in part by an increase in the abundance of the non-native amphipod *M. insidiosum* in removal samples, and a greater abundance of the oligochaetes *T. gurwitschi* (cryptogenic) and *Tubificoides brownae* (non-native)

**Table 1** List of taxa identified in this study

	Taxon	Total abundance (n = 288)	Total in reefs (n = 56)	Total in mudflat (n = 232)	Percentage in reef <sup>a</sup>	Percentage in mudflat <sup>a</sup>	Native/introduced <sup>b</sup>
<i>Monocorophium insidiosum</i>	Amphipod	54,090	38,103	15,987	90.8	9.2	I
<i>Streblospio benedicti</i>	Polychaete	23,387	374	23,013	6.3	93.7	I
<i>Thalassodrilides gurwitschi</i>	Oligochaete	22,015	557	21,458	9.7	90.3	C
<i>Melita nitida</i>	Amphipod	14,109	13,487	622	98.9	1.1	I
<i>Tubificoides brownie</i>	Oligochaete	9285	407	8878	16.0	84.0	I
<i>Grandidierella japonica</i>	Amphipod	6433	140	6293	8.4	91.6	I
<i>Capitella</i> sp.	Polychaete	4023	143	3880	13.2	86.8	C
<i>Hemigrapsus oregonensis</i>	Crab	1391	1286	105	98.1	1.9	N
<i>Dipolydora socialis</i>	Polychaete	927	435	491	78.6	21.4	N
<i>Gemma gemma</i>	Clam	436	5	431	4.6	95.4	I
<i>Nebalia gerkenae</i>	Leptostracan	375	34	341	29.2	70.8	N
<i>Sinelobus</i> sp.	Tanaid	301	286	15	98.7	1.3	I
<i>Boccardiella hamata</i>	Polychaete	283	1	282	1.4	98.6	N
<i>Eteone californica</i>	Polychaete	238	13	225	19.3	80.7	N
<i>Heteromastus filiformis</i>	Polychaete	119	0	119	0.0	100.0	C
<i>Allorchestes angusta</i>	Amphipod	93	35	58	71.4	28.6	N
Syllidae	Polychaete	31	1	30	12.1	87.9	
<i>Leptochelia</i> sp.	Tanaid	19	2	17	32.8	67.2	N
Notonectidae	Insect	18	0	18	0.0	100.0	
<i>Cirratulus</i> sp.	Polychaete	16	7	9	76.3	23.7	C
<i>Sphaeroma quoianum</i>	Isopod	16	13	3	94.7	5.3	I
<i>Boccardia proboscidea</i>	Polychaete	12	1	11	27.4	72.6	N
<i>Heptacarpus</i> sp.	Shrimp	11	0	11	0.0	100.0	
<i>Batillaria attramentaria</i>	Snail	9	3	6	67.4	32.6	I
<i>Alderia modesta</i>	Sea slug	8	1	7	37.2	62.8	N
<i>Polydora cornuta</i>	Polychaete	5	1	4	50.9	49.1	I
<i>Ianiropsis serricaudis</i>	Isopod	3	0	3	0.0	100.0	I
<i>Maera similis</i>	Amphipod	2	0	2	0.0	100.0	N
<i>Cumella vulgaris</i>	Cumacean	1	0	1	0.0	100.0	N
<i>Ampithoe</i> sp.	Amphipod	1	1	0	100.0	0.0	
<i>Exosphaeroma inornata</i>	Isopod	1	0	1	0.0	100.0	N
Total		137,658	55,336	82,321			

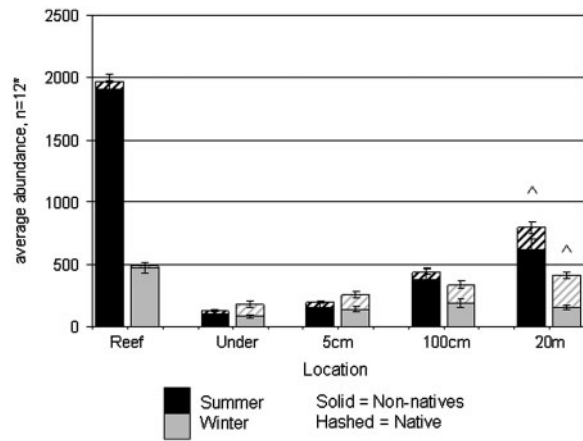
<sup>a</sup>Percent reported after standardizing by amount (weight) of reef material.

<sup>b</sup>N, native; I, introduced or non-native; C, cryptogenic [of unknown origins (Carlton 1996)]. Organisms not identified to species were only categorized as N, I, or C if enough information was available for reliable categorization.

in control and disturbance-control samples as compared to removal samples. The differences in assemblages between experimental treatment and the controls are more apparent in samples from under and near reefs with assemblage differences decreasing in the 100 cm samples, suggesting that the influences of the reef on mudflat communities have a limited spatial extent.

There was no significant effect of treatment on the percent of non-native species in the mudflats

adjacent to the non-native reefs. However, the four-way interaction term season  $\times$  time  $\times$  treatment  $\times$  distance is nearly significant ( $F=2.72$ ,  $df=8$  and  $108$ ,  $P=0.0273$ ; non-significant after Dunn-Šidák corrections adjusted significance level for multiple tests) (Table 2). This nearly significant interaction seems to be driven by a trend for increased percentage of non-natives in the winter treatments where reefs were removed, with a trend for a greater percentage of non-natives in the samples



**Fig. 2** The abundances of natives and cryptogenics (hashed) and non-natives (solid) in samples from different locations and dates, before experimental manipulation. Reef abundances are averaged after standardization by the weight of reef material sampled. ^“20 m” are averages of infauna in eight cores from the reference mudflats collected 1 year after all other samples but from the same season. Error bars show standard error.

**Table 2** ANOVA results for total abundance of organisms in infaunal samples and percent non-natives in infaunal samples. Terms were considered significant if  $P < 0.0253$  (Dunn–Šidák correction for two ANOVA tests).

Source	df	Total abundance			Percentage non-natives		
		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	<b>0.0234</b>	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	<b>0.0069</b>	1225.34	11.98	<b>0.0000</b>
Distance (di)	2	590.29	16.15	<b>0.0004</b>	466.81	4.62	0.0325
Se × ti	2	1753.98	62.81	<b>0.0000</b>	3226.30	8.21	<b>0.0057</b>
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	<b>0.0001</b>
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	<b>0.0094</b>	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	0.0273
RES	108	29.27			102.32		
Total	215						

With Dunn–Šidák correction, factors and interactions are significant below  $P = 0.0253$ .

from the under and 100 cm locations as compared to samples from the 5 cm location (Fig. 5d–f). Increases in the abundance of the non-native polychaete *S. benedicti* and the non-native amphipod *M. insidiosum* are responsible for the observed increase in non-native taxa in these samples. The ANOVA for the percentage of each sample comprised of non-natives has two significant interaction terms after Dunn–Šidák corrections: time × reef ( $F = 3.84$ ,  $df = 12$  and  $108$ ,  $P = 0.0001$ ) and season × time ( $F = 8.21$ ,  $df = 2$  and  $12$ ,  $P = 0.0057$ ) (Table 2). This is partially explained by the trend for samples in the winter to have lower percent non-natives as compared to samples in the summer (Figs 2 and 5), and for the highly variable between reef percent non-natives before and 6 months after treatment in the winter experiment (Fig. 5d and e).

### Discussion

*Ficopomatus enigmaticus* forms reefs that are structurally stable over time, providing complex three-dimensional habitat in a soft sediment environment. This biogenic habitat hosts an abundant associated fauna, distinct from nearby mudflats in species composition and relative abundance. 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, suggesting that *F. enigmaticus* may facilitate these non-natives and allowing their abundances to increase locally. In addition to providing habitat for species directly associated with the biogenic structures, non-native reefs also influence assemblages living in nearby mudflats by decreasing infaunal abundance and altering infaunal assemblage structure. Thus, the reefs’ influence also extends to nearby habitat, increasing spatial heterogeneity in faunal abundance and distribution.

The highly abundant assemblages associated with the non-native reefs are significantly different from assemblages in nearby and distant mudflats. However, nearly all species encountered were found in both habitat types, and differences in community structure between habitats are due to variation in relative abundance of species, not to differences in species composition. In fact, the same suite of common species, primarily small mobile generalists, 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 associated species. Differences in relative abundances,

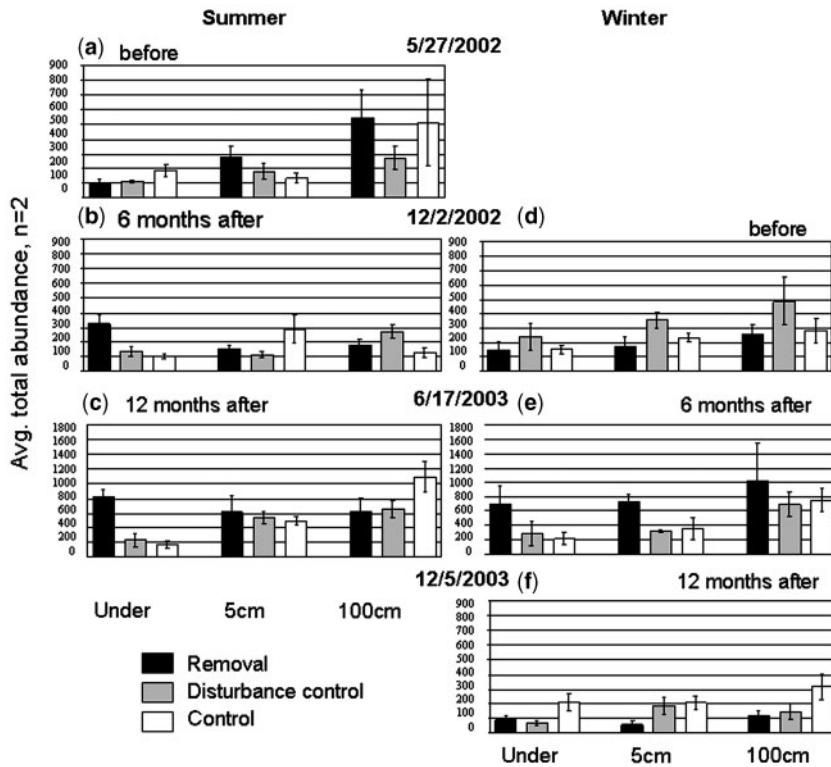


Fig. 3 Total infaunal abundance in mudflat samples from specific locations and experimental treatment groups. The date for each sampling period is listed above the graphs. (a) Summer samples taken before experimental manipulation. (b) Summer samples taken 6 months after experimental manipulation. (c) Summer samples taken 1 year after experimental manipulation. (d) Winter samples taken before experimental manipulation. (e) Winter samples taken 6 months after experimental manipulation. (f) Winter samples taken 1 year after experimental manipulation.

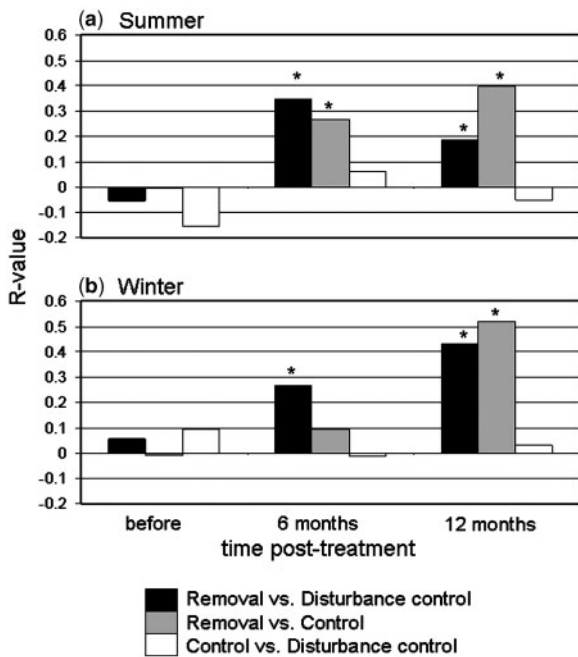
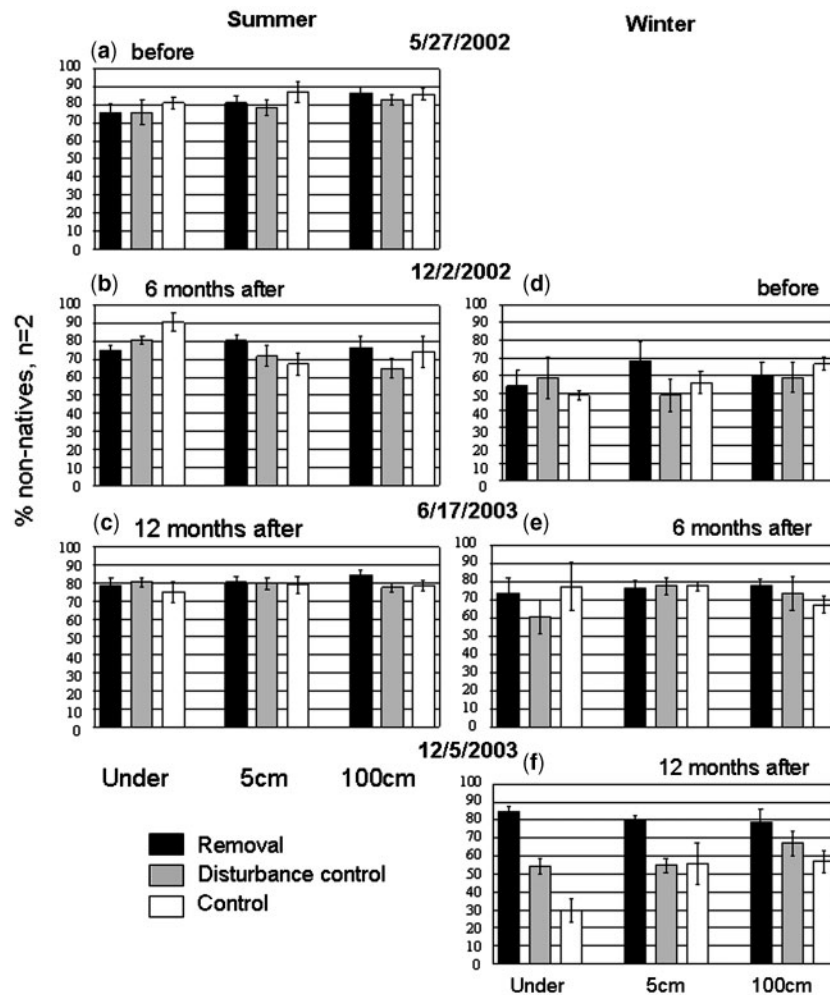


Fig. 4 R-values from ANOSIM analysis of square root transformed Bray–Curtis dissimilarities of treatment group pairs at specified times post experimental manipulation. (a) Summer samples, (b) winter samples. Asterisk indicates significant R-values.

however, suggest that recruitment and survival of some of these generalists differ between the two habitat types. Of particular interest, all non-natives found in association with the *F. enigmaticus* reefs were also found in the samples from mudflats, implying that all associated non-natives would exist in the environment regardless of whether or not the *F. enigmaticus* reefs were present.

There are a number of general facilitative mechanisms attributed to ecosystem engineers that could enhance invertebrate recruitment and survival in the *F. enigmaticus* reef matrix. The reefs, which are complex intertwined tube structures, may provide shelter from predators such as shore birds and fish. The reefs may also enhance retention of propagules, as the two most common reef crustaceans are amphipods, *M. insidiosum* and *M. nitida* and thus brood their young. These juvenile amphipods would be released within the reefs, increasing the local abundance of these species. This potential facilitative mechanism is supported by our observation of many juvenile amphipods in the samples collected from the reefs during the summer.



**Fig. 5** Percent non-native species in mudflat samples from specific locations and experimental treatment groups. The date for each sampling period is listed above the graphs. (a) Summer samples taken before experimental manipulation. (b) Summer samples taken 6 months after experimental manipulation. (c) Summer samples taken 1 year after experimental manipulation. (d) Winter samples taken before experimental manipulation. (e) Winter samples taken 6 months after experimental manipulation. (f) Winter samples taken 1 year after experimental manipulation.

Through experimental removal of reefs, we found that the reefs influence infaunal assemblages, resulting in decreased abundances near reefs as compared to areas only 1 m away from the edges of reefs. The reefs' impact seemed to be limited spatially to assemblages under and adjacent (within 5 cm) to 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 *S. benedicti* and the cryptogenic oligochaete *T. gurwitschi*. 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 *S. benedicti*, *Polydora socialis* and *Boccardia* species. Davies and colleagues measured the filtration

rate of a *F. enigmaticus* population in Marina da Gama, South Africa ( $8.59 \text{ ml mg}^{-1} \text{ worm h}^{-1}$ ) and calculated that local populations could filter all the water in this 2 m deep by 32.6 hectares estuary in  $\sim 26 \text{ h}$  (Davies et al. 1989). It is possible that *F. enigmaticus* reefs could affect the local abundance of food particles suspended in the water column. Conversely, accumulations of fecal material under and around reefs could lead to hypoxic or anoxic conditions within sediments, thereby decreasing local infaunal abundances. Local accumulation of organic matter is also suggested by the higher abundances of several detritivore species in our experiment, including the oligochaetes *T. gurwitschi*, and *Tubificoides brownae*, in the disturbance-control and control samples as compared to the removal



samples especially in the removal experiment begun in the summer. An alteration in the amount of detritus in local environments has been implicated in alterations of communities associated with other non-native ecosystem engineers 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. 2006).

*Ficopomatus enigmaticus* reefs may also indirectly structure local infaunal assemblages by harboring predators or scavengers that feed on fauna or cause physical disturbance in the surrounding environment. Biotic interactions have been linked to changes in assemblage structure associated with *F. enigmaticus* in Mar Chiquita Coastal Lagoon, Argentina (Schwindt 2001). In the Argentinean system, *F. enigmaticus* reefs attract and support high densities of the native crabs, *Cryptograpsus angulatus*. Increased predation by crabs on epifaunal and infaunal invertebrates caused significant changes in assemblages in mudflats within a 20 cm 'halo' of the reefs (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, *H. oregonensis*. Unlike the Argentinean crab, *H. oregonensis* is an omnivore, feeding mostly on algae and diatoms (Morris et al. 1980). However, *H. oregonensis* may structure infaunal assemblages near the reefs by frequent excavations that disturb local sediments.

No non-native species were found exclusively associated with the reefs, implying that the presence of *F. enigmaticus* has not resulted in any new invasions of species in Elkhorn Slough, one of the predictions of invasional meltdown (Simberloff and Von Holle 1999). There is also no indication that the presence of the non-native reefs alters the percentage of non-natives in the nearby infaunal assemblages. Many of the non-natives in Elkhorn Slough are ubiquitous and highly abundant throughout the system. Some infaunal non-natives are found in high abundance near the reefs but other non-natives are more common in mudflats away from reefs, resulting in no overall change in the percentage of non-natives in mudflats around the reefs through the course of the experiment. 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, indicating that reefs may negatively impact rather than facilitate infaunal assemblages.

However, the highly abundant non-native species associated with the reefs suggest the possibility of

positive interactions between associated non-native species and the reef itself. The reefs provide hard substrates, which are otherwise limited in mudflat environments. The two common vectors introducing species into Elkhorn Slough, oyster culture and boat-hull fouling, may have selected for a suite of species that associate preferentially with hard substrates during some phase of their lives. Our results indicate that this mechanism may explain patterns of abundance for some of the species introduced to Elkhorn Slough via introduction of hard substrates, but not for other species introduced via similar vectors. Three species (*M. insidiosum*, *M. nitida*, and *Sinelobus* sp.) that were found in greater abundances in the reefs as compared to the mudflats (Table 1) were introduced to Elkhorn Slough through associations with oysters used in local aquaculture operations (Wasson et al. 2001). For these species, the provision of hard substrates by the non-native tube-worm may lead to increased abundance, one component of invasional meltdown (Simberloff and Von Holle 1999). However, other species also introduced through associations with oysters were more abundant in the mudflat environment (e.g., *S. benedicti*, *Grandidierella japonica* and *Gemma gemma*). None of these species is dependent obligatorily on hard substrate, but each may exhibit different relationships with and responses to hard structures. Recruitment and survivorship of benthic invertebrates are influenced by a suite of processes and information beyond the identity of proposed vectors of introduction is needed to understand why some non-natives are found frequently associated with the reefs and others with the mudflats.

The non-native *F. enigmaticus* is an ecosystem engineer that provides a novel habitat used primarily by other non-native species and that alters assemblage composition in adjacent native habitats (i.e. mudflats). Non-native ecosystem engineers, including seagrasses, salt marsh plants, oysters, and mussels (Posey 1988; Crooks and Khim 1999; Ruesink et al. 2005; Brusati and Grosholz 2006) may have disproportionate impacts on invaded marine environments compared to other non-natives because of their influence on physical conditions and biological communities, in some cases leading to facilitation of other non-natives or invasional meltdown (Simberloff and Von Holle 1999). Given limited resources, a focus on controlling non-native ecosystem engineers through early detection and efforts at eradication may provide a cost-effective strategy for reducing the negative impacts of species introductions of species to coastal marine ecosystems.

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