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## Decreased solar radiation and increased temperature combine to facilitate fouling by marine non-indigenous species

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Studies of the effects of climate changes on marine biofouling have mainly focused on the effects of temperature increase, but a decrease in the level of solar radiation could also influence the establishment and persistence of fouling species. To test if decreased solar radiation and/or increased temperature influenced marine fouling communities, solar radiation, and temperature were manipulated by deploying shading devices in the intertidal zone of a central California estuary. Non-indigenous species (NIS) recruiting to artificial substrata had greater coverage under the shading treatments than under transparent plates, indicating that low radiation facilitates recruitment and growth of NIS. In contrast, the coverage of NIS underneath warmer black plates was higher than that on white plates. Furthermore, spatial comparisons of recruitment showed that NIS had a tendency to grow better in the warmer region of the estuary whereas native species showed the opposing trend. The results suggest that both lower radiation and higher temperature may facilitate the spread of marine NIS.

**Keywords:** climate change; fouling community; non-indigenous species; global dimming; solar radiation; temperature

### Introduction

Marine fouling species found in the coastal regions of the world cause significant economic impacts by fouling ships and man-made structures (Cohen & Carlton 1998; Pimentel et al. 2000; Bax et al. 2003; Weigle et al. 2005; Schultz et al. 2011). Among those fouling species, the spread of non-indigenous species (NIS) is a well-established threat to biodiversity (Bax et al. 2003; Piola & Johnston 2008; Davidson et al. 2009; Sorte et al. 2010). Many NIS generally fail to survive in the new environment and do not succeed in reproducing. In some cases, however, species can adapt to a new environment and establish reproductive populations (Cohen & Carlton 1998; Ruiz et al. 2000; Stachowicz et al. 2002; Dafforn et al. 2009; Sorte et al. 2010).

Current climate change is regarded as one of the driving forces that contribute to the spread of marine fouling NIS by conferring a competitive advantage to species adapted to the changed environments, and by influencing the establishment and spread of NIS. A growing number of studies suggest that an increasing temperature can facilitate recruitment and persistence of marine NIS that are tolerant to temperature change or originally from warmer regions (Sagarin et al. 1999; Stachowicz et al. 2002; Harley et al. 2006; Sorte et al. 2010; Zerebecki & Sorte 2011).

However, increasing temperature is not the only phenomenon related to climate change that may alter the

community structure. Change in the amount of solar radiation could be another driver of change within biological communities. Recent studies have documented a trend of decreased incident sunlight radiation, or ‘global dimming’ (Stanhill & Cohen 2001; Wild et al. 2005; Wang et al. 2009). Reviews of global dimming report that the average radiation decrease over 1973–2007 is  $0.51 \pm 0.05 \text{ Wm}^{-2}$ , which is equivalent to a reduction of 2.7% per decade (Stanhill & Cohen 2001; Wang et al. 2009). Increasing cloud cover due to increased levels of aerosol is regarded as the main cause of dimming (Stanhill 1998; Power 2003). Even with the high uncertainty regarding future levels of incident radiation and debate over the consistency of the trend of global dimming (Wild et al. 2005, 2007), a continued decrease is expected to affect primary productivity and surface earth energy balance (Roderick 2006; Mercado et al. 2009). Lower light levels may also influence animal communities by increasing the recruitment, growth, and survival of sciophilous species. Fouling species which do not have shells or crust are expected to have low endurance to high solar radiation and UV irradiance. Therefore, lower radiation might benefit them by facilitating recruitment and growth. In contrast, photosynthetic species such as algae can benefit from higher solar radiation by increased photosynthetic activities.

In this paper, whether decreased solar radiation and/or increased temperature might influence the establishment

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and persistence of marine fouling NIS and change in the community structure is explored by examining recruitment and growth of fouling species in an estuary located in central California, USA. Although there are several studies on the effect of decreased level of solar radiation on marine and estuarine organisms and communities (eg Wethey 1984; Glasby 1999; Struck et al. 2004; Miller & Etter 2008), no study has investigated whether a decrease in solar radiation might influence the recruitment and growth of fouling NIS in the invaded region. A decreased level of solar radiation can also interact with temperature changes that are known to facilitate establishment and persistence in NIS (Sagarin et al. 1999; Stachowicz et al. 2002). This paper examines whether a change in solar radiation and temperature influence the recruitment and growth of marine fouling NIS by manipulating solar radiation levels and temperatures on recruitment substrata. Firstly, different shading devices were deployed to determine if solar radiation influences NIS. Secondly, the effect of an increase in temperature in facilitating the recruitment and growth of NIS was investigated by manipulating the temperature of substrata. Thirdly, the coverage of NIS and native species on recruitment tiles deployed in various sites with different temperature variation was compared to further test if higher temperature can facilitate the spread of NIS.

## Materials and methods

### Study site and community

The study was conducted from April through September 2009 and 2010 in Elkhorn Slough, Monterey Bay, in central California, USA. The maximum tidal height is  $\sim 2$  m and the minimum height is  $\sim -0.5$  m. The light and temperature manipulation experiments were conducted, in both years, in an intertidal mudflat of the upper estuary (near Azevedo Pond) ( $36^{\circ}50'33''\text{N}$ ,  $121^{\circ}44'58''\text{W}$ ). In 2009, recruitment rates were also quantified at 14 sites throughout Elkhorn Slough (Figure 1 and Table 1). Fifty-eight NIS have been reported in Elkhorn Slough to date, and the upper estuary is more invaded by exotic species than the lower estuary (Heiman et al. 2008; Wasson 2010). Because hard substrata are more heavily invaded than soft bottoms in the intertidal areas of Elkhorn Slough (Wasson et al. 2005), the focus was on fouling species colonizing hard surfaces.

### Shading experiment

To determine if decreased radiation influences recruitment, growth, or survival of NIS, a shading experiment was conducted. Solar radiation was manipulated using opaque plastic screens. Shading screens were  $30 \times 30 \times 0.5$  cm acrylic transparent or opaque plates (see below). Screens were attached to PVC frames using 10 cm cable ties weaved through two evenly spaced

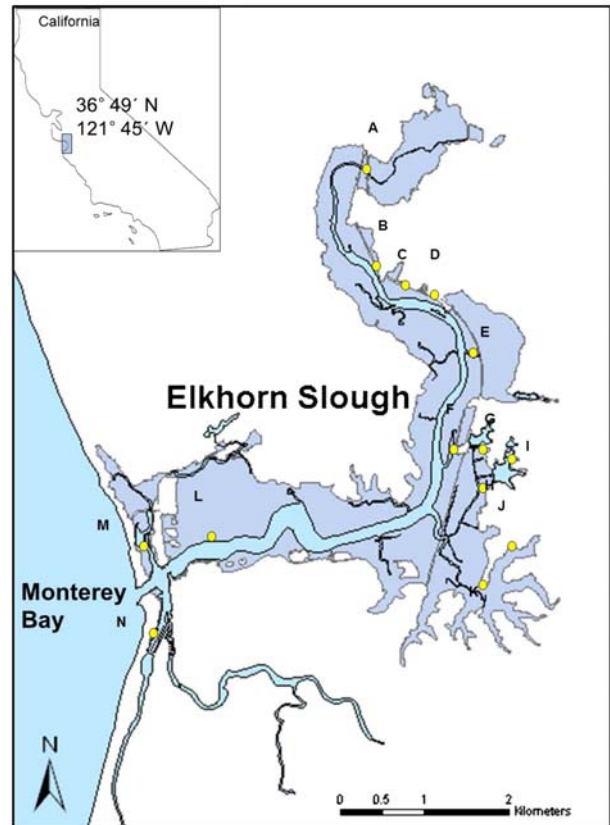


Figure 1. Fourteen sites in Elkhorn Slough where the recruitment of species was compared. Site C was also used for shading and heating experiments.

Table 1. Name and GPS coordinates of the 14 sites in Elkhorn Slough.

	Site name	GPS coordinates
A	Hudson's Landing	N36°51.376'W121°45.293'
B	Azevedo Pond, Upper	N36°50.647'W121°44.210'
C	Azevedo Pond, Lower	N36°50.556'W121°44.960'
D	Kirby Park	N36°50.456'W121°44.666'
E	North Marsh Exit	N36°50.080'W121°44.309'
F	Whistle Stop Lagoon	N36°49.439'W121°44.389'
G	Humming Bird Island	N36°49.433'W121°44.564'
H	South Marsh Bridge	N36°49.209'W121°44.225'
I	South Marsh East	N36°49.260'W121°44.029'
J	Parsons Slough Overlook	N36°48.478'W121°44.301'
K	Five Fingers Boardwalk	N36°48.730'W121°44.060'
L	Moss Landing Wildlife Area Trail	N36°48.790'W121°46.817'
M	Moss Landing State Park	N36°48.919'W121°47.402'
N	Salinas River State Beach	N36°47.965'W121°47.331'

Note: The letters in the first column correspond to those in Figure 1.

5 mm diameter holes drilled 10 mm away from each screen side. PVC frames were constructed as follows: four 20 cm-long PVC pipes were jointed with elbow joints to make a square frame. Then four 30 cm-long

PVC pipes were inserted into the joints to support the square structure.

Each screen was placed, in the field, above a recruitment tile. Recruitment tiles (10 × 10 cm tumbled slate tiles) were attached to 10 × 10 cm plastic rebar caps with polyurethane Gorilla Glue<sup>®</sup>. The latter is known to be toxic when it is in liquid form (<http://www.gorillatough.com>), but when it hardens after giving off vapor, it becomes waterproof and less likely to be toxic to the marine environment. The minimum amount of glue was applied to the other face of the recruitment tiles and it did not appear to have any toxic effect on the recruiting species. Rather, fouling species grew well on the edge side of tiles where remnants of glue might have been present. It is possible that the glue may attract fouling species, though this effect would be similar across all treatments.

Then 30 cm long rebar posts were inserted into rebar caps. Recruitment tiles were supported by rebar posts inserted into the sediment to a depth of 25 cm, at +1.0 foot tidal height. The rebar caps were exposed out of the mudflat surface. Seven rows of 4 recruitment tiles were each marked perpendicular to the direction of tide flow. Recruitment tiles were separated by 50 cm.

To create treatments of varying light levels, both black and white opaque screens were deployed. Black screens absorb all radiant energy whereas white screens reflect short wave lengths of light. Thus, it was expected that lower light (and possibly lower temperatures) would appertain under black than white screens. To determine if the plate *per se* and not the resulting alteration of light and temperature influenced the recruitment of invasive species, a transparent screen was also deployed as a procedural control. Finally, another set of recruitment tiles was left exposed to natural sunlight and was not covered with a screen as a control (Figure 2a). Seven replicates of each treatment were constructed. Using a randomized grid design, each group of treatments was located at the same height perpendicular to the tidal flow. Temperature loggers (I-button<sup>®</sup>) placed in water-proof capsules were attached on the side of two random recruitment tiles in each treatment and temperature was recorded at 30 min intervals throughout the experiment. Each shading screen was cleaned with a sponge every 1–2 weeks to remove sediments and fouling species. Every month, between 17 April and 18 September 2009, during daytime low tides falling below +1.0, the surface of each tile was photographed with a digital camera (Canon Powershot Pro 1), and temperature loggers were retrieved and replaced. The solar irradiance at the surface of each tile was measured using a light meter (Li-250A, Li-COR<sup>®</sup>) between 11:00 and 16:00 h on 12 random days during the experiment. Concurrently, UV levels (UV513AB, General<sup>®</sup>) were measured. The experiment was terminated after the study site was covered by water continuously for a

month, resulting in screens that were heavily fouled by both organisms and sediment.

### **Heating experiment**

Since temperature was dependent on solar radiation in the shading experiment, an additional experiment was conducted where the direction of the interaction between temperature and solar radiation was changed. In this experiment, recruitment between the underside of black and white acrylic plates used as screens in the shading experiment was compared (Figure 2b). The plates had the same effect of blocking solar radiation as in the previous experiment, but the temperature of black plates was generally higher than those of white plates, due to the former absorbing more radiation energy. Therefore, recruitment that occurred directly on the underside of black and white plates was compared to recruitment on tiles placed under the screening treatments in order to elucidate how the interaction between solar radiation and temperature influence the recruitment of NIS by decoupling these two factors.

On 20 June 2010, when the mudflat was exposed to air, eight 30 × 30 × 0.5 cm black and eight white acrylic plates were placed ~5 cm above the surface of the intertidal mudflat at the tidal height of +30 cm. Each of eight rows was marked at 60 cm intervals perpendicular to the tidal flow. Using a randomized grid design, each group of black and white plates was located in each row. Each plate was supported by a 30 cm-long rebar post, attached at the center of each plate with a rebar cap (10 × 10 cm), glued to the plate using Gorilla Glue<sup>®</sup>. Every 2 weeks, the upper surface of each plate was cleaned to remove sedimentation and other fouling materials. Every month, between 20 June and 18 October 2010, during daytime low tides falling below +30 cm, the underside of each plate was photographed with a digital camera. Temperature loggers (I-button<sup>®</sup>) were attached to the underside of two plates in each treatment and temperature was recorded at 30 min intervals throughout the experiment. Temperature loggers were retrieved and replaced every month.

### **Comparison between sites with different temperature variation**

The heating experiment above can only manipulate the temperature of the plates exposed to air and solar radiation. To determine how temperature influences larval recruitment and growth of fouling species, identical recruitment surfaces were additionally deployed at the 14 sites from the upper to the lower estuary of Elkhorn Slough (for the location, see Figure 1). As a recruitment base, each 10 × 10 cm tumbled slate tile was attached to a 10 × 10 cm rebar caps with gorilla glue<sup>®</sup>. A 30 cm long rebar was inserted into each rebar cap. At the +30 cm tidal level at each site, 6 recruitment tiles supported by

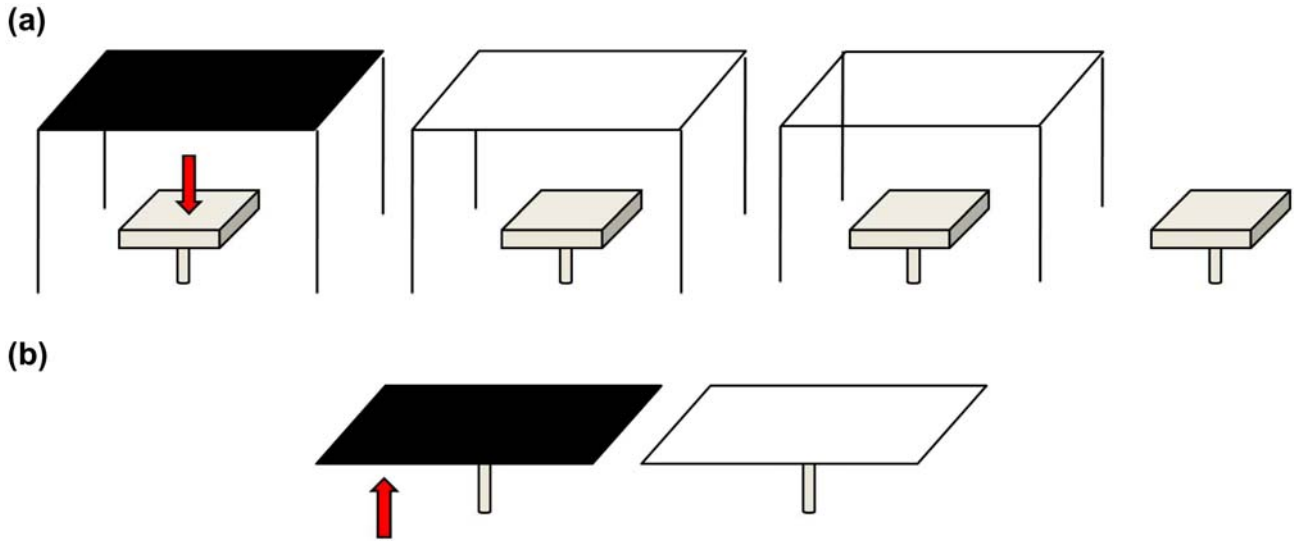


Figure 2. Schematic diagram of (a) shading experiment and (b) heating experiment. Arrows indicate the surface where the attached species assemblages were observed.

rebar were inserted into the sediment. In order to measure the temperature variability in each site, two I-buttons<sup>®</sup> were attached on the edge of two of the recruitment tiles and temperature was recorded at 30 min intervals. The temperature loggers were retrieved every month to check variation in temperature. The salinity of water was separately measured twice using a salinity meter (Lutron<sup>®</sup> YK-31SA) at each site at the same tidal height when tides covered the tiles. Every month, between 17 April and 18 September 2009, during low tides falling below +30 cm during daytime, the surface of each tile was photographed with a digital camera and species were identified and species coverage was analyzed in the laboratory.

#### *Species identification and statistical analysis*

Species were generally identified from photographs using taxonomic keys including: for invertebrates Morris et al. (1980), Carlton (2007), Cohen (2011) and Intertidal Invertebrates of the Monterey Bay Area, California (<http://www.seymourcenter.ucsc.edu/Inverts/>); for algae: Abbott and Hollenberg (1976) and Mondragon and Mondragon (2003). In cases of uncertainty, samples were examined under a microscope and the identification was confirmed using the Light and Smith Manual (Carlton 2007). Whether they were natives or of non-indigenous status was assigned using the classification of Wasson et al. (2001, 2005). The only sponge complex that could not be identified was recorded as 'unknown' sponge species, because it is impossible to identify the sponges correctly without molecular analysis (Fuller & Hughey Forthcoming). The percentage coverage by each species

or frequency in the fouling community on the recruitment tiles was measured using the software Image J<sup>®</sup> with a resolution of  $2272 \times 1704$ . For the serpulid polychaete *Ficopomatus enigmaticus* and the orange-striped green anemone *Diadumene lineata*, the number of individuals was also recorded. Because the proportional coverage data were not distributed normally, data were arcsine square root transformed prior to analysis. For the shading and heating experiments, repeated measures ANOVAs were used to test whether there were differences in the percentage cover of each species among experimental treatments (shading experiment: control, transparent, black and white screens, heating experiment: black and white plates). The assumption of equal between-group correlations and group variances ('sphericity') was also tested using Mauchley's sphericity test; sphericity was not violated in any variables (all  $p > 0.05$ ). To determine significant differences among treatments, a Tukey's honestly significant difference (HSD) *post hoc* test was used. To further examine the possible effects of experimental treatments on the community structure (ie in the relative abundances of different species), ANOSIM and SIMPER analyses using PRIMER ver. 6 was also conducted. These analyses were performed on the data in the final month of observation of recruitment when the coverage of NIS was the highest.

For comparison of species coverage among sites, the mean coverage of NIS and native species assemblages on the tiles for each site was calculated and then a Spearman rank correlation was used to determine if temperature of each site influenced the coverage of NIS and native species assemblages.

## Results

### Solar radiation and temperature

Solar radiation both under the transparent screens (mean  $\pm$  SD =  $86.3 \pm 16.1 \text{ W m}^{-2}$ ,  $N=12$ ) and without screens ( $97.2 \pm 14.4 \text{ W m}^{-2}$ ) was greater than under the shading (black and white) screens (Wilcoxon signed rank test, all  $p < 0.0001$ ). There was significantly higher solar radiation under white screens ( $12.2 \pm 1.9 \text{ W m}^{-2}$ ) than under black screens ( $3.3 \pm 0.4 \text{ W m}^{-2}$ , Wilcoxon signed rank test:  $Z = -3.059$ ,  $p = 0.002$ , Figure 3a). UV radiation showed the same trends as solar radiation under the various treatments (Figure 3b). The white screen treatment effectively mimics the effect of clouds on solar irradiance: irradiance under white plates on sunny days ( $17.5 \pm 1.4 \text{ W m}^{-2}$ ) was not significantly different from natural irradiance on cloudy days ( $17.7 \pm 5.2 \text{ W m}^{-2}$ , Mann-Whitney  $U$ -test:  $U_{5,6} = 12$ ,  $Z = -0.548$ ,  $p = 0.5839$ ).

During low tides, when the mudflats were exposed to air and sunlight, the temperature on the recruitment tiles was also influenced by the screens (Figure 3c and d). The average temperatures of tiles under transparent screens (mean  $\pm$  SD =  $20.1 \pm 5.2 \text{ }^\circ\text{C}$ ) and without any screens ( $20.0 \pm 5.0 \text{ }^\circ\text{C}$ ) were about  $2.0 \text{ }^\circ\text{C}$  higher than under the shading treatments (black:  $18.2 \pm 4.0 \text{ }^\circ\text{C}$ , white:  $18.4 \pm 4.0 \text{ }^\circ\text{C}$ ; paired  $t$ -test: transparent vs white screens,  $t_{306} = -9.675$ ,  $p < 0.0001$ ). There was no significant difference in temperature between the tiles covered by transparent plates and those without screens (paired  $t$ -test:  $t_{306} = 0.651$ ,  $p = 0.515$ ). Temperatures 5 cm under black screens were significantly lower than under white screens (paired  $t$ -test:  $t_{306} = 4.544$ ,  $p < 0.0001$ , Figure 3b and c). This effect of opaque plastic screens on temperature might be due to the different filtering of sunlight radiation by black vs white screens (Figure 3a). In contrast, the temperature of the underside of black screens ( $17.9 \pm 2.7^\circ$ ) was significantly higher than that of white screens ( $16.7 \pm 2.4^\circ$ ) when the screens were exposed to air and sunlight, during daytime low tides (paired  $t$ -test:  $t_{12} = 6.040$ ,  $p < 0.0001$ ).

### Solar radiation effect on recruitment success

Two months after the recruitment tiles were deployed in the field, there was no visible colonization except for a thin layer of the native green alga *Ulva linza* on the tiles under the transparent screens and control tiles without screens (100% coverage for both treatments), but not under the opaque screens. Starting in July 2009 (3 months after the start of the shading experiment), however, *U. linza* disappeared and four NIS colonized the recruitment tiles over the following 2 months (Figure S1a–d). [Supplementary material is available via a multimedia link on the online article webpage.] Two bryozoan species, *Bugula neritina* (unknown origin) and *B. stolonifera* (from Europe), were the most abundant species. The serpulid

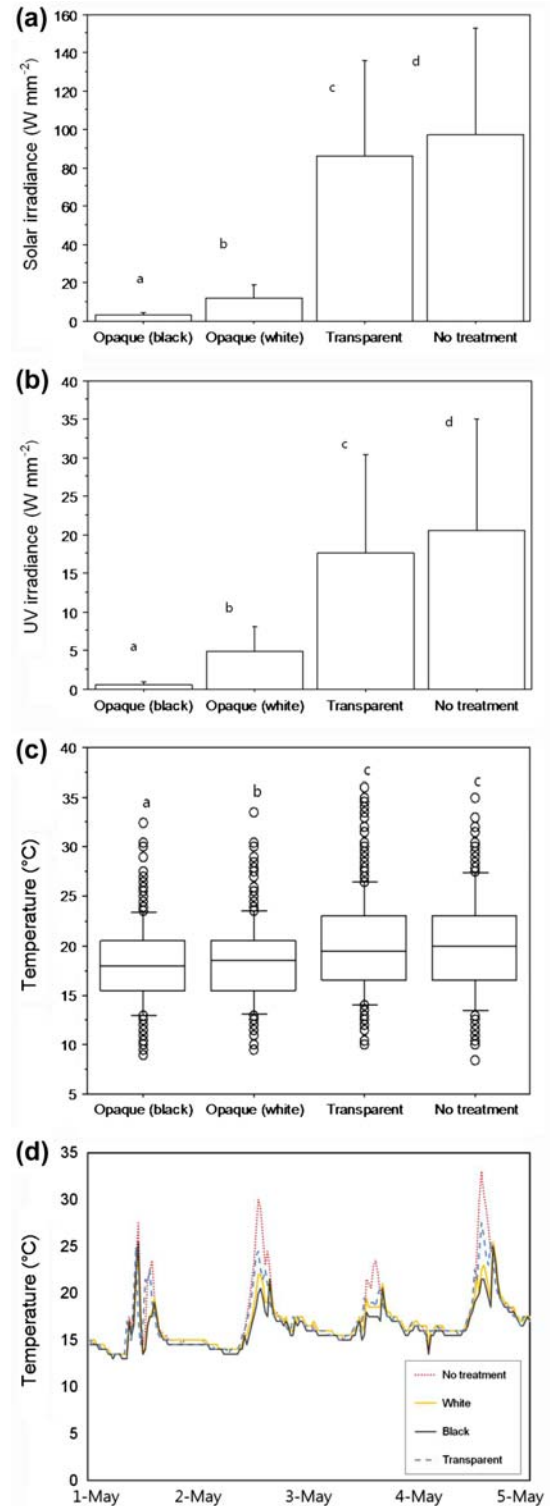


Figure 3. Average ( $\pm$  SD,  $N=12$ ) (a) solar irradiance, (b) UV irradiance on the recruitment tiles in each shading treatment, (c) temperatures under each shading treatment when tiles were exposed to air during the experiment, and (d) 4-day time series of temperatures on recruitment tiles in each treatment. Different letters on the bars represent a significant difference between treatments.

polychaete *F. enigmaticus* (unknown origin) was the third most abundant NIS that recruited, followed by the orange-striped green anemone, *D. lineata* (from the Western Pacific) which had the lowest average percentage cover among the four species. The native species Olympia oyster (*Ostrea lurida*) recruited on only one tile (1 individual ~1% coverage) under a white screen.

There was a significant effect of solar radiation and temperature on the coverage of NIS assemblages (Figure 4a, repeated measures ANOVA; light × month:  $F_{3,24}=8.069$ ,  $p<0.001$ ). *Post hoc* multiple comparison tests revealed that the coverage of NIS, in months 3–4 of the experiment, was higher under the white and black screens than in controls (Tukey HSD; Black vs No treatment:  $p=0.02$ , White vs No treatment:  $p<0.0001$ ). The coverage of NIS was significantly higher under white screens than under black screens ( $p=0.006$ ). There was no difference in the total coverage of NIS under the transparent screens and on the no treatment control ( $p=0.957$ ).

Solar radiation clearly influenced the coverage of the two bryozoan species, *B. neritina* (Figure 4b, repeated measures ANOVA; light × month:  $F_{3,24}=8.069$ ,  $p<0.001$ ) and *B. stolonifera* (Figure 4c, light × month:  $F_{3,24}=6.087$ ,  $p=0.003$ ). *Post hoc* tests revealed that starting in month 3 of the experiment, the coverage of *B. neritina* was higher under white screens than under transparent screens (Tukey HSD;  $p<0.0001$ ) or under

black screens (Tukey HSD;  $p=0.006$ , Figure 4c), with no significant difference in coverage between black and transparent screens ( $p=0.07$ ). The coverage of *B. stolonifera* was also higher under the white screens than under the transparent screens (Tukey HSD;  $p<0.0001$ , Figure 4c) and under black screens ( $p=0.006$ ), and similar between black and transparent screens ( $p=0.417$ ). Trends in abundance of the *F. enigmaticus* among treatments were similar to those observed in the bryozoan species (Figure 4d, effect of light:  $F_{3,24}=1.967$ ,  $p=0.145$ ; light × month:  $F_{3,24}=6.108$ ,  $p=0.223$ ). Similarly, there was a significant interactive effect of light and month on the abundance of the orange-striped green anemone *D. lineata* (Figure 4e, Repeated measures ANOVA;  $F_{3,24}=3.131$ ,  $p<0.05$ ).

On the final month of the recruitment experiment, when the coverage of fouling species was the highest (August 2009), fouling community structure was significantly different among treatments (ANOSIM:  $R=0.379$ ,  $p<0.001$ ). Pairwise tests revealed significant difference between all treatment combinations ( $p<0.01$ ) except under black and white screens. *B. neritina*, *B. stolonifera*, and *D. lineata* accounted for 32.9, 27.5, and 24.4% of the dissimilarity between black and transparent treatments, 41.2, 21.6, and 20.1% between white and transparent treatments, 30.21, 35.21, and 21.24% between black screens and unshaded controls, and 36.54, 31.84, and 18.50% between white screens and unshaded

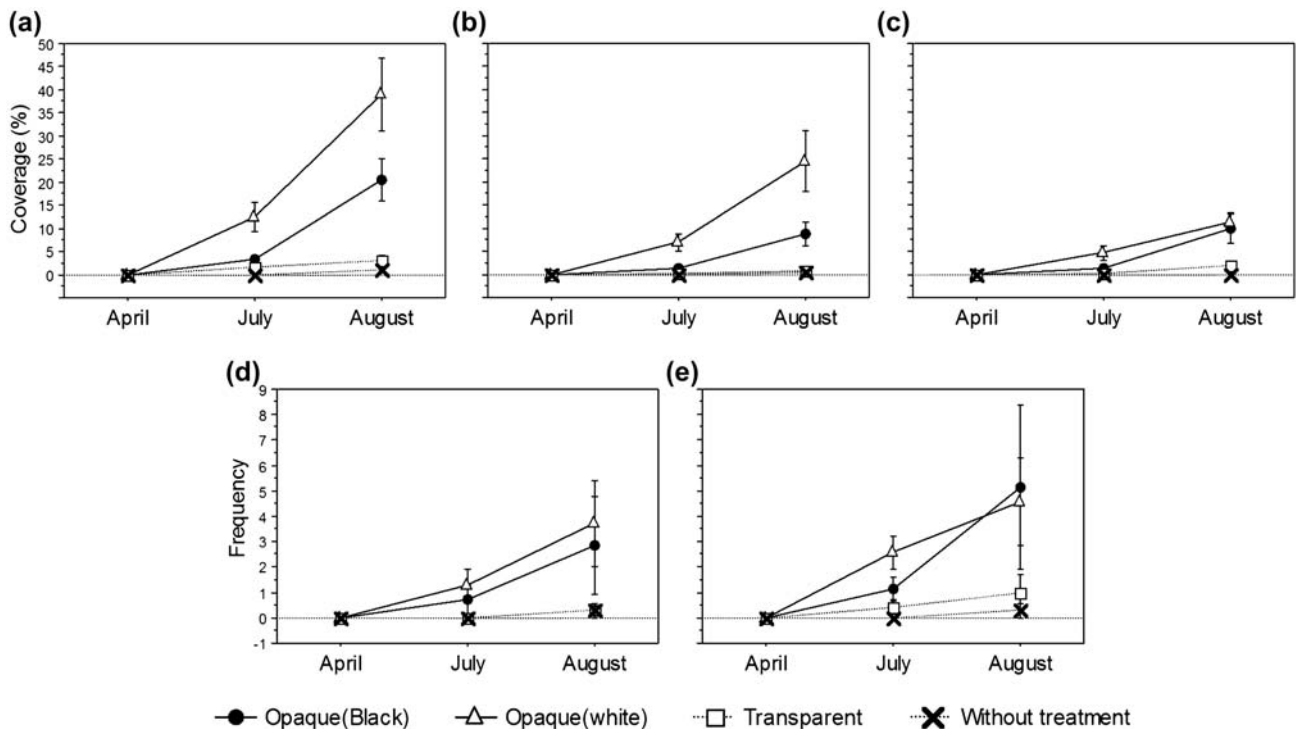


Figure 4. Change in the coverage (mean ± SE,  $N=7$ ) of (a) total NIS assemblages, (b) the bryozoans *B. neritina* and (c) *B. stolonifera* and in the frequency of (d) the serpulid polychaete *F. enigmaticus*, and (e) the orange striped green anemone *D. lineata* on the recruitment tiles under different shading treatments.

controls. Thus, *Bugula* spp. drove most variation in fouling community structure.

### Temperature effect on recruitment success

A total of 5 species, the 3 species which recruited in the previous experiment (*B. neritina*, *B. stolonifera*, and *F. enigmaticus*) and 2 additional species (the bryozoan *Cryptosula pallasiana* and unknown sponges) were found during the second experiment (Figure S1e and f). The overall coverage of NIS on the underside of the black plates was higher than on the underside of the white plates (Figure 5a and Table 2). The coverage of 2 dominant species (*B. neritina*: Figure 5b, *B. stolonifera*: Figure 5c) was higher on the underside of the black plates than on the underside of the white plates in months 3 and 4 of the experiment. *F. enigmaticus* (Figure 5d) and *C. pallasiana* (Figure 5e) also showed similar trends. In contrast, the coverage of unknown sponges showed the opposite trend but not at a significant level (Figure 5f).

ANOSIM revealed significant differences in community structure between the two treatments in the final month of recruitment ( $R=0.357$ ,  $p=0.003$ ). *B. neritina*, *B. stolonifera*, *F. enigmaticus*, *C. pallasiana*, and unknown sponges contributed 26.89, 24.45, 20.69, 13.53, and 10.25% to dissimilarity, respectively.

### Correlation of species coverage with temperature

The temperature time series varied among sites (Figure 6). In total, 6 NIS and 4 native species colonized the recruitment tiles at the 14 sites (Table 3). The most abundant NIS was *B. neritina* and *F. enigmaticus*. The most common native species was the green algae *Ulva fenestrata*. Five months after the recruitment tiles at the 14 sites was set up, there was a significant trend of increasing total coverage of NIS with an increasing mean 3-month temperature at the sites (Spearman rank correlation:  $\rho$  corrected for ties = 0.690, Tied  $Z=2.512$ ,  $p=0.01$ , Figure 7) though each NIS species coverage was not significantly correlated with temperature. This trend persisted for 3 months. The coverage of native species (mostly composed of *U. fenestrata*) showed the opposite trend. As the mean temperature increased, the coverage of native species decreased (Spearman rank correlation:  $\rho$  corrected for ties = -0.713, Tied  $Z=-2.422$ ,  $p=0.015$ ). The mean daily temperature maxima ( $\rho$  corrected for ties = 0.645, Tied  $Z=2.326$ ,  $p=0.02$ ) and the mean daily temperature minima ( $\rho$  corrected for ties = 0.542, Tied  $Z=1.953$ ,  $p=0.05$ ) also had a positive correlation with the coverage of NIS. The temperature variability (standard deviation of temperature time series) did not influence the coverage of NIS ( $\rho$  corrected for ties = 0.357, Tied  $Z=1.289$ ,  $p=0.198$ ). Salinity was not correlated with the coverage of NIS ( $\rho$  corrected for

ties = 0.107, Tied  $Z=0.372$ ,  $p=0.710$ ). A mean temperature between 18 and 19 °C appears to be the threshold temperature for both NIS and native species to recruit on the tiles. No NIS successfully colonized the tiles below this mean temperature, whereas very few native species colonized above this mean temperature (Figure 7).

### Discussion

This study provides the experimental evidence that both solar radiation and temperature can influence the spread of abundant marine fouling NIS in a Californian estuary. Decreased solar radiation and increased temperature significantly increased the overall coverage of marine non-indigenous fouling species during the summer and early fall in Elkhorn Slough. The results complement recent findings that temperature increase facilitates the establishment and persistence of marine NIS (eg Harley et al. 2006; Sorte et al. 2010). In addition, the results indicate that decreased solar radiation, another potential component of climate change, can also significantly influence the spread of marine fouling NIS. These results highlight the importance of considering the combined effects of multiple stressors associated with climate change though the small number of species examined here prevents broad generalization of these effects beyond the present system.

Site comparisons further suggest that increasing temperature enhances recruitment and growth of marine fouling NIS with the abundance of NIS positively correlated with temperature. In the experimental system, however, only a small number of species (5 NIS and 4 native species) colonized the recruitment plates, preventing direct comparison of effects between NIS and native species. In particular, two of the four native species were algae whereas all the NIS were invertebrates. Thus, the different responses documented may reflect functional differences between algae and invertebrates, rather than between natives and NIS. Further studies comprising controlled comparisons between multiple native and non-indigenous taxa (eg Stachowicz et al. 2002; Sorte et al. 2010) are needed to assess whether increasing temperature and decreasing solar radiation differentially affect these species groups and their competitive abilities.

It should be noted that the present study focuses on the change in the abundance and community structures of fouling species rather than competitive interaction between NIS vs native species. The increased coverage of NIS under screens may be due to the blockage of UVB that can cause direct damage to some of marine fouling species. Because strong UVB radiation can generally have a negative effect on marine species (Harley et al. 2006; Bancroft et al. 2007), blockage of UVB can facilitate the recruitment, and growth of fouling NIS. Fouling species living in the intertidal area are



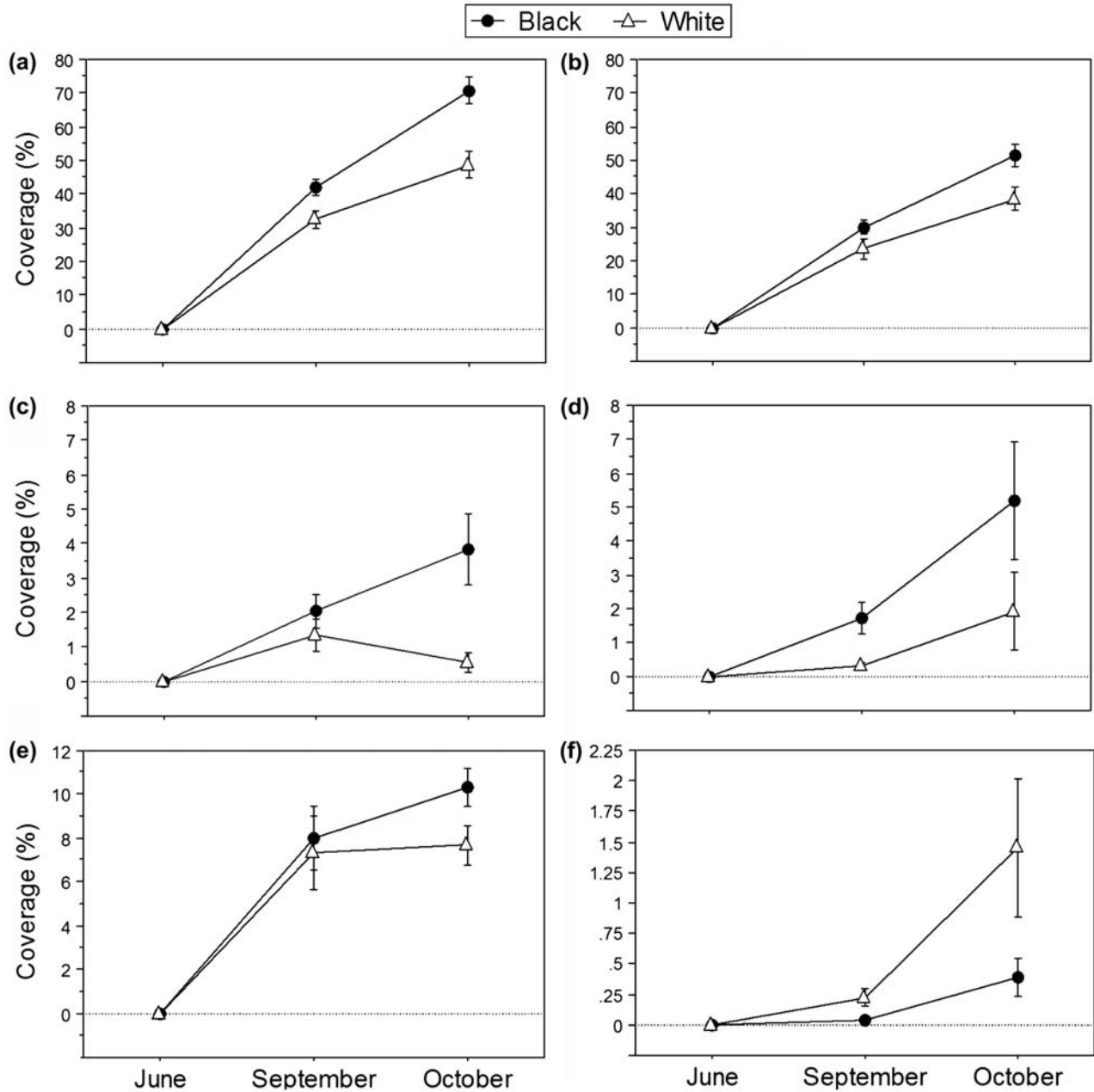


Figure 5. Change in the coverage (mean  $\pm$  SE,  $N=8$ ) of (a) NIS assemblages, (b) *B. neritina*, (c) *B. stolonifera*, (d) *F. enigmaticus*, (e) *C. pallasiana*, and (f) unknown sponges on the underside of black and white plates. Note that the scale of coverage on the y-axis was not applied identically to each species.

Table 2. Statistical analysis of the effect of plates and interaction with months on the coverage of species in the temperature manipulation experiment.

Species	Effect of plates	Plates $\times$ month
Overall coverage of NIS	$F_{1,14} = 17.292, p = 0.001$	$F_{1,14} = 9.838, p < 0.001$
<i>Bugula neritina</i>	$F_{1,14} = 7.377, p = 0.017$	$F_{1,14} = 2.464, p = 0.139$
<i>B. stolonifera</i>	$F_{1,14} = 7.586, p = 0.016$	$F_{1,14} = 6.224, p = 0.026$
<i>Ficopomatus enigmaticus</i>	$F_{1,14} = 3.723, p = 0.074$	$F_{1,14} = 1.091, p = 0.314$
<i>Cryptosula pallasiana</i>	$F_{1,14} = 1.634, p = 0.222$	$F_{1,14} = 0.641, p = 0.437$
Unknown sponges	$F_{1,14} = 3.950, p = 0.067$	$F_{1,14} = 2.491, p = 0.137$

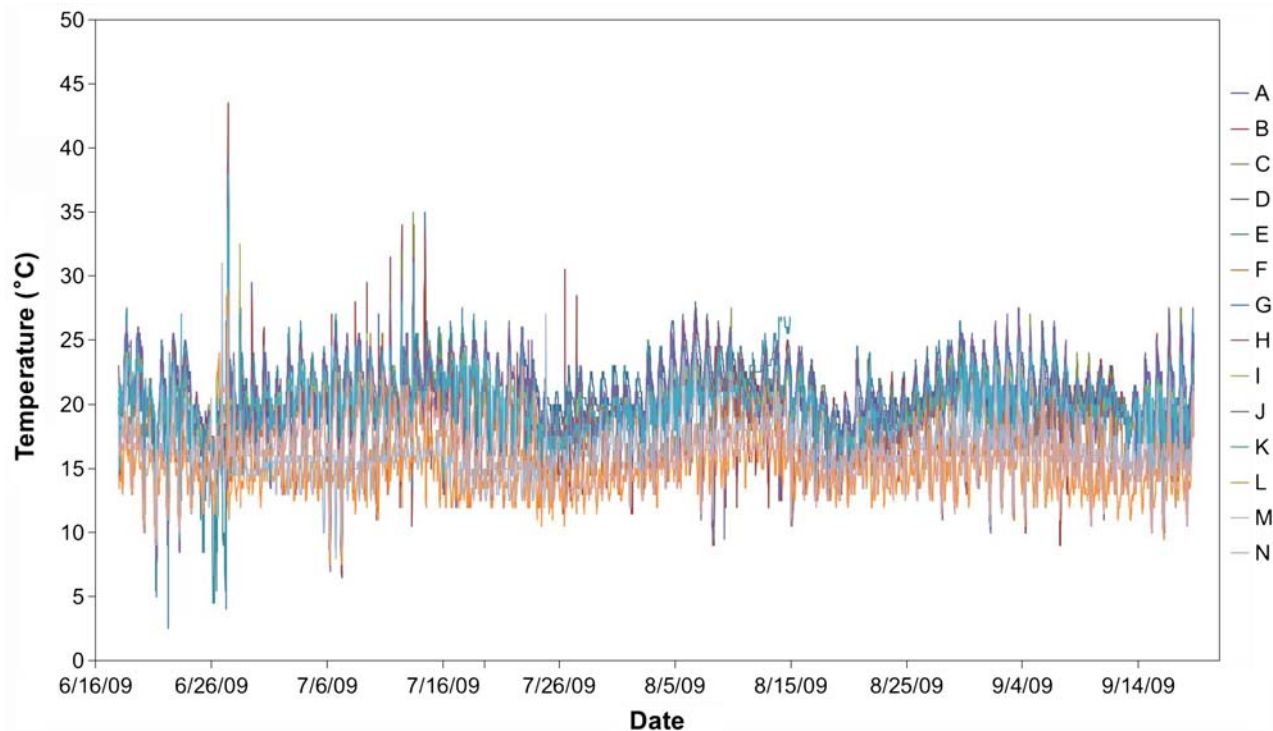


Figure 6. Temperature time series of the 14 sites during the 3 month period 18 June to 18 September 2009. The letters on the right hand side correspond to those in Table 1.

Table 3. List of NIS and native species that colonized the recruitment tiles at the 14 sites in Elkhorn Slough.

	Common name	Species name	Phylum	Relative abundance (% of total coverage)
NIS	Bryozoan	<i>Bugula neritina</i>	Bryozoa	25.4
	Serpulid polychaete	<i>Ficopomatus enigmaticus</i>	Annelida	21.5
	Orange striped green anenome	<i>Diadumene lineata</i>	Cnidaria	4.3
	Colonial asidian	<i>Botrylloides violaceus</i>	Chordata	0.15
Native	Green alga	<i>Ulva fenestrata</i>	Chlorophyta	46.7
	Green alga	<i>Ulva linza</i>	Chlorophyta	1.6
	Barnacle	<i>Balanus glandula</i>	Crustacea	0.07
	Olympia oyster	<i>Ostrea lurida</i>	Mollusca	0.15

exposed to air and sunlight for a maximum of 6 h daily, depending on tidal cycles. To survive in this habitat, organisms must be able to withstand temperature extremes and desiccation. Nevertheless, strong sunlight and exposure to UV radiation might be damaging as indicated by the result that NIS survived and grew better under shades. In previous studies, *B. neritina* also had greater survival under lower illumination (Dahms et al. 2007). Shaded substrata could also be colonized preferentially by larvae that have an orientation bias to escape predation, as most naturally dim places are crevices and cracks. Indeed, bryozoan larvae have phototactic responses at first, but become photonegative later in their development (Ryland 1960; Pires & Woollacott 1997). Such recruitment preference may be selected for, due to

improved survival in dimmer places. Increased coverage of NIS under shades could also be due to other effects of dimming. Shaded places have no or limited algal cover. Macroalgae can compete for space with other sessile organisms. A thin coverage of the native alga *U. linza* on the tiles during the initial experimental period might have deterred larval recruitment to the tiles.

Interestingly, coverage of NIS did not increase linearly with decreasing solar radiation. The coverage of three NIS, *B. neritina*, *B. stolonifera*, and *F. enigmaticus*, was higher under the white screens than under the black screens, despite the small difference in solar radiation below the two different screen types. White screens mimicked the condition of solar radiation on the cloudy days and the result suggests that the projected decrease

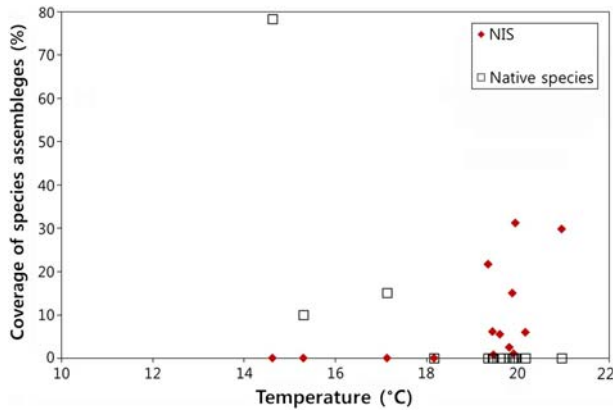


Figure 7. Relationship between the 3-month mean temperature and the mean coverage of NIS and native species assemblages on the 6 recruitment tiles set in 14 sites of Elkhorn Slough.

in solar radiation may influence the spread of fouling species significantly. However, the opaque screens used in the shading experiment manipulated solar radiation and temperature in the same direction, causing a reduction of both variables under white screens, and an even greater reduction under black screens. The result of greatest recruitment under white screens, not under black screens, suggests that these two factors may interact in their effects on NIS, and that these species may benefit from simultaneous decreased radiation and increased temperature.

The results of the additional heating experiment confirm this conclusion by showing that the coverage of the same 3 fouling species (*B. neritina*, *B. stolonifera*, and *F. enigmaticus*) was greater on the underside of black acrylic plates which have lower radiation but higher temperature than white plates. Taken together, these results suggest that both black and white screens blocked harmful UVB that can influence the biological performance of NIS (Williamson et al. 2001), and that the temperature difference between the two treatments led to differences in the coverage of fouling species through a positive effect of increased temperature on metabolic rates, resulting in greater growth rate (Stachowicz et al. 2002; Sorte et al. 2010; Smale et al. 2011). However, there is a possibility that the different colors of plates influenced the recruitment of fouling species (eg Swain et al. 2006; Su et al. 2007).

Most species found in this study are also abundant in subtidal areas and aerial exposure and filtering of solar radiation by overlying water might be influential to the patterns that were observed. Indeed, the manipulation of solar radiation and temperature is likely to affect NIS only when they are exposed to air on sunny days. Exposure to harmful UVB and desiccation during low tides significantly influence the physiological performance of multiple intertidal species (Shick & Dykens 1984;

Helmuth 2002; Gilman et al. 2006). The result of the heating experiment, however, also indicates that NIS can grow even when they are exposed to air and warm temperatures, and that they may benefit from these conditions.

Except for the recruitment of green algae during the first 2 months of the shading experiment, recruitment of native species on the tiles in the manipulation experiments was very limited, although some sessile native species such as the Olympia oyster *O. lurida* did occur at the site. Historically, substrata in Elkhorn Slough were soft sediments (mud) rather than hard materials. Artificial construction, such as bridges, jetties, and ripraps, has significantly increased the proportion of hard substrata in the system (Wasson et al. 2005; Heiman et al. 2008) and provided additional habitats favorable for fouling NIS recruitment (Heiman et al. 2008). The use of hard materials (acrylic plates and slates) for recruitment substrata may have favored NIS in a similar manner (Tyrrell & Byers 2007; Dafforn et al. 2012). In addition, recruitment of native species may be low in this system because of the current low densities and fecundity of adults (Heiman et al. 2008; Wasson 2010). Alternatively, low recruitment of native species could also be due to high temperature at the experimental site. This possibility was supported by the result of the comparison of species coverage among locations with different temperature variations. Though other variables may influence the spread of NIS, no evidence was found that salinity influenced recruitment and growth of fouling species. Whereas the coverage of NIS was higher at the sites with a high mean temperature, native species recruited only at the sites with a mean temperature lower than 18 °C. Where native species recruited, NIS were very rare. Though different responses of natives and NIS in this study are unlikely to be produced *via* competitive interactions, the results of the heating experiment and the site comparison together supports the hypothesis that temperature increase can facilitate the spread of fouling NIS after invasion, possibly through a direct effect of these variables on NIS recruitment and growth.

Temperature and light availability can vary through processes other than climate change. Increased temperature accompanied by changing water stream flows with constructions might create favorable conditions for NIS establishment and spread. Based on the results, it is proposed that increased water turbidity in Elkhorn Slough, associated with altered flows and high erosion rates (Breaker et al. 2008) may also significantly increase the spread of NIS. Changes in temperature and radiation can benefit some of marine fouling NIS primarily because NIS from warmer and possibly dimming regions may have greater survival and growth in environments that are changing in a similar direction. An increase in temperature is known to increase the spread of NIS, because

a warmer temperature is more suitable to the physiology of those NIS with warm affinity (Stachowicz et al. 2002; Sorte et al. 2010). A decrease in radiation will also benefit NIS without protective structures, such as shells, which have less tolerance to harmful UVB. In contrast, native species may not compete well with NIS under decreased solar radiation regimes. Moreover, organisms that photosynthesize such as algae do not benefit from decreased radiation and are expected to respond differently than invertebrates, both for native and NIS. The results suggest that multiple environmental changes, including climatic changes and the addition of artificial substrata to coastal and estuarine ecosystems, are likely to increase the spread of NIS, and associated economic costs of managing and controlling fouling species.

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