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Impacts of a simulated heat wave on composition of a marine community

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Extreme events, such as heat waves, are predicted to increase in frequency, duration, and severity as a consequence of climate change. However, global change research generally focuses on increases in mean temperatures and fails to address the potential impacts of increasingly severe heat waves. In addition, climate change may interact with another primary threat to biodiversity, non-native species invasions. We assessed the impacts of a short-term heat wave on the marine epibenthic fouling community of Bodega Harbor, California, USA, by exposing experimental mesocosms to a simulated heat wave in the laboratory and then monitoring community development in the field. We hypothesized that (1) juveniles would be more susceptible to heat waves than adults, (2) native species would be more susceptible than non-native species, and (3) non-native species would recover more quickly than native species. We observed no effect of the heat wave on juvenile species richness, either initially or during the recovery period, relative to communities at ambient seawater temperatures. In contrast, total adult species richness initially declined in response to the heat wave. Adult community composition also changed in heat-wave treatments, with non-natives representing the majority of species and occupying more cover than native species. The reduction in native richness associated with the heat wave persisted through the recovery period, whereas invasive richness was actually higher on heat-wave versus ambient plates at 95 days. Heat waves have the potential to alter the composition of this community because of species-, taxon-, and/or origin-specific responses; for example, non-native bryozoans displayed greater resistance than native and non-native tunicates. Recovery from the heat wave occurred via growth of resistant individuals and larval recruitment. Our study highlights the importance of considering species' and community responses to heat waves, and not just mean predicted temperature increases, to evaluate the consequences of climate change.

Global climate change and non-indigenous species are two of the greatest threats to biodiversity and ecosystem functioning (Vitousek et al. 1997, Sala et al. 2000, Halpern et al. 2008). Both climate change and introduced species have had wide-ranging community-level impacts on species' abundances, distributions and interactions, and they have resulted in local extinctions (Vitousek et al. 1997, Ruiz et al. 2000, Walther et al. 2002, Rosenzweig et al. 2007). In addition to their direct effects, climate change and invasions may interact. For example, climate-change conditions are predicted to favor – and thus facilitate the spread of – non-native species (Dukes and Mooney 1999, Byers et al. 2002, Stachowicz et al. 2002). Sala et al. (2000) point out that "interactions among the causes of biodiversity change … represent one of the largest uncertainties in projections of future biodiversity change". Here, we address this potential interaction by assessing the impacts of a simulated heat wave on native and non-native species in a marine community.

Heat waves are extreme high temperature events that are predicted to increase in severity and frequency as a consequence of global climate change (Karl and Trenberth 2003, Meehl and Tebaldi 2004, Meehl et al. 2007). Heat waves are typically defined as a period of at least three to five days during which mean or maximum temperature anomalies of at least 3–5°C above normal are observed (Meehl and Tebaldi 2004, Meehl et al. 2007). Although the great majority of climate change studies focus on the effects of increases in mean global temperature (Easterling et al. 2000, Jentsch et al. 2007), extreme events such as heat waves have the potential to significantly and abruptly alter biotic systems (Easterling et al. 2000, Parmesan et al. 2000). Studies of the impacts of extreme events are typically either (1) observational, with researchers relating dynamics in long-term datasets to unforeseen events that occurred during data collection (Swaty et al. 2004, Daufresne et al. 2007, Harris et al. 2007, Jöhnk et al. 2008), or (2) experimental, with treatments designed to mimic field-relevant extreme conditions (Bassow et al. 1994, de Valpine and Harte 2001, Van Peer et al. 2004). Most community-level studies of heat wave impacts have been conducted in terrestrial systems, and only a handful of observational (Sutherland 1970, Harley 2008, Oxenford et al. 2008) – and even fewer experimental

(Glynn and D'Croz 1990, Allison 2004) – studies have been carried out in marine systems. Studies in all systems have shown that responses to heat waves are generally species-specific (Parmesan et al. 2000, de Valpine and Harte 2001, Mouthon and Daufresne 2006, Miriti et al. 2007, Petes et al. 2007, Harley 2008), and heat waves can essentially 'reset' community development when complete mortality occurs (Allison 2004, Miriti et al. 2007). In addition, impacts often persist after conditions return to ambient levels, either for months (Bassow et al. 1994, Oxenford et al. 2008), for years (Miriti et al. 2007), or even longer, such as with range shifts (Easterling et al. 2000, Fleischer et al. 2007, Harris et al. 2007, Jentsch et al. 2007).

A less pronounced response of non-native species to heat waves would be consistent with two prevailing paradigms in invasion biology. First, disturbance is predicted to facilitate invasions via one or more of the following mechanisms: an increase in resources, a decrease in native competitors or predators, or a shift in conditions that favors non-natives (Byers et al. 2002, Clark and Johnston 2005, Olyarnik et al. 2009). The 2003 European heat wave was associated with shifts in community structure in both freshwater (Daufresne et al. 2007) and marine communities (Neumann et al. 2009). Daufresne et al. (2007) suggest that creation of open space by this heat-wave disturbance allowed the colonization and increased abundance of non-natives in a macroinvertebrate community in the French Rhône River. This example highlights a limitation of using observational studies to infer climate impacts on species invasions: because both the rates of climate change and invasions are increasing over time due to direct anthropogenic forcing (Carlton 2001, Rosenzweig et al. 2008), it is difficult to parse out temporally-covarying effects from interactive effects. This confounding effect of the covariation between time, climate change, and invasions can be avoided with experimental studies (White et al. 2001) or those that compare interspersed 'warm' and 'cold' years (Stachowicz et al. 2002). The potential for heat waves to facilitate the increase of non-natives depends on the robustness of a second paradigm: that non-native species are able to tolerate a broader range of temperatures than native species, a pattern that derives from evidence for a direct relationship between range width (in terms of latitude and climate) and invasiveness (Dukes and Mooney 1999, Chown et al. 2007; but see Holway et al. 2002). For example, Petes et al. (2007) found that responses to a natural heat wave differed between a native and a non-native mussel species, with native and non-natives experiencing 35% and 3% mortality, respectively. Generally, few data allow the assessment of this paradigm, making it difficult to extrapolate to the community level.

We investigated heat-wave impacts in a marine epibenthic fouling community, which has historically been a model system for community ecology studies (Sutherland 1974, Sutherland and Karlson 1977) and is an ideal system for studying the relationship of climate change and species invasions, in particular. Fouling species (e.g. bryozoans, tunicates [sea squirts], hydroids and polychaetes) colonize human-made structures including ships' hulls, docks, and submerged pipelines, in addition to occurring on natural hard substrata such as subtidal rocky reefs. These species therefore settle readily on artificial, experimental substrates. Recruitment is continuous during the summer, when heat waves are most likely to occur, and rapid growth contributes to rapid space occupation. Fouling communities can also be highly invaded. Non-native species now represent the majority of common species and 71% of total cover at our study site, highlighting the need for further studies to predict the trajectory of non-native species dominance in this particular community (Sorte et al. 2010b).

Since space is often the primary limiting resource in the fouling community (Stachowicz et al. 1999), processes that create bare space are important for driving species turnover and compositional changes. We conducted our heat-wave experiment using communities at two different stages of development: juvenile-dominated and adult-dominated. Juveniles tend to experience higher mortality than older individuals and be more susceptible to physiological stress (Gosselin and Qian 1997, Hunt and Scheibling 1997). However, since previous studies suggest that juveniles' lower tolerance thresholds are not often exceeded by current field conditions (Hunt and Scheibling 1997), we were interested in whether these thresholds could be exceeded in future heat-wave conditions. We also conducted our experiment on established, adult communities because adult individuals represent the majority of cover in the system, and their mortality would have a larger per capita effect on levels of bare space (Miriti et al. 2007). In both juvenile- and adult-dominated communities, acquisition of bare space takes place via a combination of new recruitment and lateral growth of established individuals and colonies.

We examined the impacts of an experimentally-induced heat wave on a typical suite of species in the Bodega Harbor (California, USA) fouling community. Intact communities were transported to the laboratory, where the heat-wave treatment was applied in mesocosms. Communities were then returned to the field for monitoring of recovery and subsequent community development. Resistance, or the magnitude of the immediate change caused by the heat wave, and recovery, or the time point at which richness and cover did not differ from levels in communities maintained at ambient temperatures, were compared for non-natives, native species, and for the community as a whole. Our a priori hypotheses were that (1) juveniles are less resistant (i.e. more susceptible) to heat waves than adult individuals, (2) non-native species are more resistant than native species, and (3) non-native species recover more quickly than native species.

Methods

Study system

Our study system was the subtidal epibenthic fouling community in Bodega Harbor, Bodega Bay, California, USA. Bodega Harbor is a shallow, marine-dominated coastal lagoon that receives minimal freshwater input (Boyd 1972, Grosholz 2005). Typical salinity is ≥33 ppt, and daily mean temperatures range between 9 and 17°C at 1 m depth (based on measurements between 2005 and 2009; Sorte unpubl.). All field deployments and surveys were conducted on floating docks at Spud Point Marina (38°32’90”N, 123°05’81”W). Vectors of species introductions are likely similar to those implicated for San Francisco Bay (Cohen and Carlton 1995), including fishing and recreational boat traffic. Most non-native fouling species observed in this study (Supplementary material Appendix 1 Table A1) are originally of Western Pacific or European origin (Cohen and Carlton 1995), and non-natives dominate the fouling community of Spud Point Marina in terms of cover and common species (Sorte et al. 2010b).

Temperature treatments

The temperature treatments were designed to reflect current ambient conditions in Bodega Harbor and a potential future heat wave. Recent heat waves in Bodega Harbor have occurred during the 1982–83 El Niño event (~+4°C, Scripps Inst. of Oceanography 1984) and during late July 2006 (~+4°C). We determined our heat-wave treatment by taking into account:

(1) the usual mean temperature of 15.0°C over the period of the experiment (Supplementary material Appendix 1 Fig. A1),
(2) the predicted increase in mean sea temperature off the central California coast of 3°C (Meehl et al. 2007),
(3) a future heat wave of 6.5°C, which accounts for the predicted increase in heat-wave severity on the northern California coast of 2°C (Meehl and Tebaldi 2004) and is within the range of published heat-wave definitions (Meehl and Tebaldi 2004, Meehl et al. 2007).

Thus, our target treatment temperatures were 15.0°C and 24.5°C (= 15.0 + 3.0 + 6.5°C).

We achieved an actual heat-wave treatment temperature of 24.7 ± 0.2°C using submersible heaters (7.5 W) which laid flat against the bottoms of the aquaria. Aquaria containing plates assigned to both treatments were dispersed randomly in a running seawater table which kept ambient plates at a temperature of 15.0 ± 0.1°C. Water temperatures were monitored by taking daily measurements in each tank using a digital handheld thermometer.

Laboratory experiment

Fouling species were collected on 10 × 10 cm PVC plastic plates suspended horizontally 1 m below the surface of the docks at Spud Point Marina. Plates were deployed in the field 10 days and 4 months prior to the start of the experiment for the juvenile and adult plates, respectively. Two experimental runs were conducted sequentially and treated as blocks in our analyses. Plates (32 total) were photographed, and all plates were counted before applying temperature treatments. For each block, adult and juvenile plates were randomly assigned to the ambient and heat-wave treatments (n = 8 per age × treatment combination, divided between the two blocks). During the experiment, plates were suspended in the same orientation as in the field (upside-down and horizontally), each in a separate 2.5-l plastic aquarium. Plates were exposed to a 12 h light/dark cycle, and tanks were constantly bubbled with air. Half (1.25 l) of the water in the tanks was replaced daily with aerated unfiltered seawater equilibrated to the treatment temperature and containing the natural phytoplankton component (as a food source). Chl a levels – an index of phytoplankton concentrations – ranged from 0.88 ± 0.21 $\mu g\ l^{-1}$ immediately after feeding to 0.72 ± 0.36 $\mu g\ l^{-1}$ the following day before the water change (when chl a should have been most depleted), based on representative measurements in four tanks. These chl a values did not differ significantly from concurrent field values (1.01 ± 0.19 $\mu g\ l^{-1}$ average of three subsamples; t-test $p > 0.5$) at Spud Point Marina. Temperatures were initially raised at a rate of ~3°C per h in the heat-wave treatment and were then kept constant during water changes. Treatments were applied for three days (block 1: 15–18 August 2008, block 2: 18–21 August 2008) after which the heat-wave plates cooled to ambient temperature at a rate of ~2°C per h. At the end of the experiment, plates were photographed and counted, as at the beginning of the experiment, and were returned to the field for subsequent monitoring of the community dynamics.

Species counts

Plate censuses (photographs and species counts) were conducted before the experiment (initial), immediately after the experiment (T = 0), and after 5, 35 and 95 days of subsequent community recovery and development. For the adult plates, percent cover was estimated based on direct visual observation for the initial, T = 0, and five day censuses and based on visual observation of digital photographs for the 35 and 95 day censuses. For the juvenile plates, species counts were based on microscope counts for the initial, T = 0, and five day censuses and visual percent cover estimates from digital photographs for the 35 and 95 day censuses.

Field plates

We compared recovery and development of lab experiment plates to background recruitment and community development on adjacent, blank field plates. Plastic recruitment plates (n = 4) identical to our experimental plates were deployed over seven sampling intervals corresponding to the recovery period of the experimental plates. At the end of each 1- to 3-week recruitment interval, plates containing recruits were removed and were replaced with clean plates. Individual recruits were counted in the lab under a dissecting microscope, and the average plate counts for each species were used to calculate recruitment rates in recruits per plate per day. Plates used as field controls (n = 3) were seasoned in the field for 10 days and were, then, scraped in the lab and redeployed on 15 August (concurrent with the start of the lab experiment). These plates were allowed to develop continuously, as with the experimental plates, for ~95 days. Censuses of field control plates (photographs and species counts) were conducted after 5, 35 and 95 days, as for the lab experiment plates. Percent cover was estimated by visual observation of digital photographs for the five day census and by direct visual observation for the 35 and 95 day censuses.

Analyses

The effects of temperature on richness and abundance (as percent cover) were analyzed for all species, and separately for natives and non-natives, at the four recovery time points. Analyses of variance (ANOVA) and repeated-measures ANOVA (RM-ANOVA) were conducted with SAS ver. 9.1 using Proc GLM. For RM-ANOVA, the most conservative adjusted degrees of freedom (time DF = 1) were used for calculating p-values for time and time × treatment. We evaluated the RM-ANOVA assumption of sphericity by calculating Mauchly's criterion, and we report Greenhouse–Geiser adjusted p-values where necessary. Block was included in all statistical analyses. Age was not a factor in any of the analyses; we ran separate analyses for juvenile and adult plates. All data are presented as means ± 1 SE.

Results

Juvenile plates

Twenty species were identified on at least one of our juvenile or adult plates, including seven natives, nine non-natives, and four cryptogenic species (Supplementary material Appendix 1 Table A1). On the juvenile plates, there was no detectable impact of the heat-wave treatment on total richness or on richness of either native or invasive species alone (RM-ANOVA $p > 0.64$; Fig. 1; Supplementary material Appendix 1 Table A2a), and the effect of the heat wave on richness did not change over time (time × treatment $p > 0.08$; Supplementary material Appendix 1 Table A2a). At the species level, the only common species for which juveniles were impacted by the heat wave was the native, colonial tunicate *Distaplia occidentalis* (hereafter *Distaplia*) which experienced a decrease in survival (based on change in cover during the experiment) in the heat-wave treatment as compared to the ambient treatment. Mortality of juvenile *Distaplia* was 40% higher in the heated than in the ambient treatment ($t = 3.60$, DF = 14, $p = 0.003$), and this impact did not appear to be a lab artifact, based on a comparison with field mortality rates (Sorte et al. 2010b; M. Cockrell unpubl.). Juvenile survival of six common non-native species was not affected by the heat wave ($p > 0.09$).

Adult plates

Species richness

There were no initial, pre-treatment differences between ambient and heated treatments for any species on the adult plates ($p > 0.1$), but the simulated heat wave caused an immediate reduction in species richness on adult plates in the heat-wave treatment as compared to the ambient treatment. This reduction was apparent for total richness ($t = 7.54$, DF = 14, $p < 0.0001$, Fig. 2a), native richness ($t = 6.78$, DF = 14, $p < 0.0001$, Fig. 2b), and invasive richness ($t = 4.00$, DF = 14, $p = 0.001$, Fig 2b).

Whereas total richness on heat-wave plates returned to ambient levels by the 35 day census (Fig. 2a), there was a shift in community composition, with non-natives contributing disproportionately to this total richness when compared to pre-treatment conditions, that persisted for at least 95 days (Fig. 2b). Overall, native richness was lower on heat-wave than ambient plates (RM-ANOVA $F_{1,13} = 43.44$, $p < 0.0001$), and the effect of the heat treatment on native richness did not change over time (time x treatment $F_{1,14} = 3.30$, $p = 0.091$, Supplementary material Appendix 1 Table A2). Native richness on heat-wave plates was still lower than on ambient plates at the 95 day census ($t = 3.92$, DF = 14, $p = 0.002$). In contrast, invasive richness on heat-wave plates not only recovered to, but actually exceeded, ambient levels by the 35 day census ($t = 2.28$, DF = 14, $p = 0.039$), a trend that continued through the duration of the experiment (Fig. 2b).

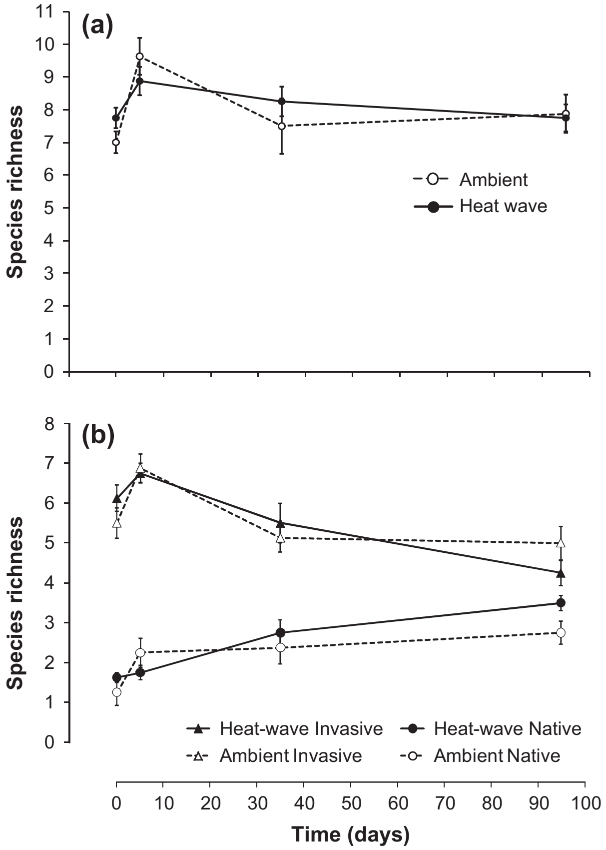

Figure 1. Changes in species richness on juvenile plates over time. The heat wave never affected juvenile species richness, either (a) for the community as a whole, or (b) when natives and invasives were considered separately. Data are means ± 1 SE. All statistical comparisons between ambient and heat-wave treatments were non-significant ($p > 0.05$).

Percent cover

Total cover was reduced by the heat wave (RM-ANOVA $F_{1,13} = 20.64$, $p = 0.001$, Supplementary material Appendix 1 Table A2c, Fig. A2) and did not recover to ambient levels until between the 35 and 95 day censuses (Fig. 3a). However, native species cover was disproportionately affected (RM-ANOVA $F_{1,13} = 13.66$, $p = 0.003$); the effect of the heat-wave on invasive cover throughout the recovery period was marginally non-significant ($F_{1,13} = 4.36$, $p = 0.057$). Invasive cover was reduced on heat-wave plates on day 5 ($t = 3.38$, DF = 14, $p = 0.005$) but recovered to ambient levels by day 35 ($t = 0.54$, DF = 14, $p = 0.595$, Fig. 3b). In contrast, the impacts of the heat wave on native cover

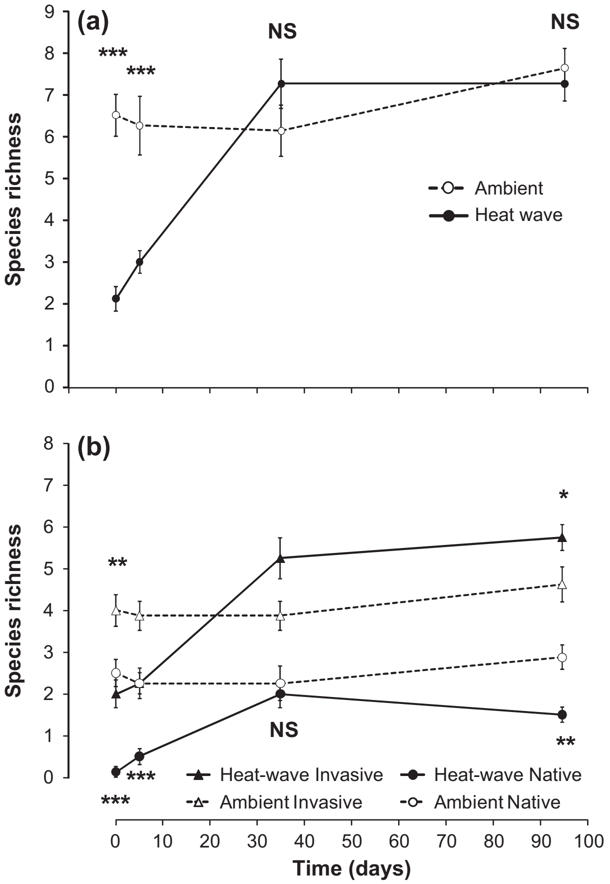

Figure 2. Changes in species richness on adult plates over time. (a) For the community as a whole, the heat wave resulted in an initial loss in richness, but at 35 and 95 days, there were no differences between ambient and heat-wave plates. (b) Whereas both native and invasive richness were initially reduced by the heat wave, invasive richness more than recovered – richness was higher in heat-wave than ambient treatments at 35 and 95 days – but native richness in heat-wave treatments never fully recovered to ambient levels, even after 95 days. Data are means ± 1 SE. Statistical comparisons between ambient and heat-wave treatments are indicated with symbols adjacent to data points: non-significant (NS), $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). In (b), upper symbols indicate comparisons of invasive species richness whereas lower symbols indicate comparisons of natives.

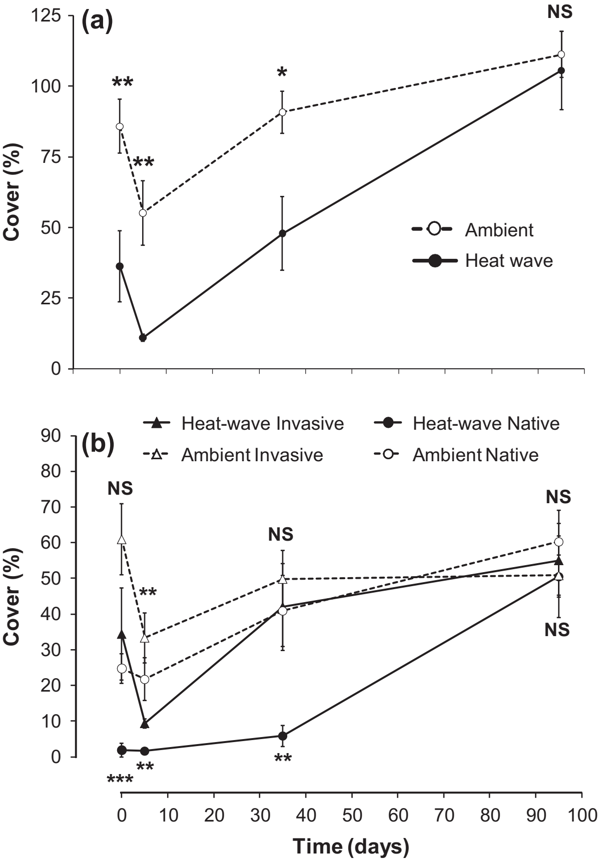

Figure 3. Changes in cover on adult plates over time. (a) For the community as a whole, the heat wave resulted in an initial loss in cover, but at 95 days, there were no differences between ambient and heat-wave plates. (b) Cover of invasive species declined at 5 days, but by 35 days, there were was no difference between ambient and heat-wave plates. The heat wave had more lasting effects on cover of native species; cover was lower on heat-wave than ambient plates at 35 days but did not differ between the treatments at the 95 day census. Data are means ± 1 SE. Statistical comparisons between ambient and heat-wave treatments are indicated with symbols adjacent to data points: non-significant (NS), $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). In (b), upper symbols indicate comparisons of invasive species cover whereas lower symbols indicate comparisons of natives.

(RM-ANOVA $F_{1,14} = 13.66$, $p = 0.003$) were still evident at day 35 ($t = 3.36$, $DF = 14$, $p = 0.005$), and native cover did not return to ambient levels until between the 35 and 95 day censuses (Fig. 3b).

Species-specific responses

Non-native species already dominate the Bodega Harbor fouling community and represented the majority of species (65%) and live cover (73%) based on averages of the initial, pre-treatment plate counts. Eight species occurred on a sufficient number of plates for statistical analysis of resistance and recovery dynamics, including six non-native and two native species (Table 1; note that there were no significant differences in initial cover for any of these species; $p > 0.1$).

The resistance and recovery of adults of individual species to the heat wave depended on the species' origins (i.e. native or non-native), higher order taxonomy, and/or growth morphology (Table 1). Non-native bryozoans, including encrusting *Watersipora subtorquata* and *Schizoporella* sp., and arborescent *Bugula neritina* species, were most resistant to the heat wave (Table 1). In fact, abundances of *Bugula* and *Schizoporella* were sometimes greater in the heat-wave treatment than in the ambient treatment (i.e. *Bugula* on day 95 and *Schizoporella* on days 5 and 35; Table 1). Non-native tunicates, including the colonial species *Botrylloides violaceus*, *Diplosoma listerianum* and *Didemnum vexillum*, all experienced ~100% mortality in the heat-wave treatment (i.e. 0% cover for *Botrylloides* and *Diplosoma* on day 0 and for *Didemnum* on day 5, once dead material had sloughed off the plates). However, treatment differences were not significant for *Diplosoma* or *Didemnum* due to high variability in the cover on ambient plates.

Table 1. Percent cover for each of the eight most common fouling species on adult plates in ambient (Amb) and heat-wave (HW) conditions.

			Recovery time (days)§									
			Initial		0		5		35		95	
Species	Taxon†	Origin‡	Amb	HW	Amb	HW	Amb	HW	Amb	HW	Amb	HW
Bugula	B	I	2.2	2.4	2.2	2.5	3.8	2.1	0.9	5.1	**3.9**	**10.4***
Watersipora	B	I	6.5	4.2	6.5	6.1	6.4	3.8	13.1	10.1	11.9	12.6
Schizoporella	B	I	0.4	2.3	0.2	1.6	**1.8**	**6.9***	**2.4**	**25.4****	0.6	4.7
Botrylloides	T	I	45.1	34.7	**45.9**	**0.0*****	**20.3**	**0.1****	12.0	21.4	4.8	6.4
Diplosoma	T	I	7.8	9.9	2.9	0.0	4.1	0.5	13.7	18.7	6.2	9.6
Didemnum	T	I	1.7	25.2	2.5	25.6	3.9	0.0	11.1	3.1	12.9	6.6
Ascidia	T	N	7.0	4.1	9.1	2.1	**13.0**	**1.4***	**37.9**	**4.2****	46.8	40.5
Distaplia	T	N	21.8	14.7	**15.2**	**0.0*****	**8.8**	**0.0****	3.7	0.1	0.8	0.0

†B = Bryozoan, T = Tunicate; ‡ I = Invasive (non-native), N = Native; §Significant differences between ambient and heat-wave conditions, based on t-tests, are indicated in bold and with asterisks: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

While they were not as resistant as non-native bryozoans, non-native tunicates recovered faster than native tunicates; abundances of all three non-native tunicate species on heat-wave plates were not significantly different from ambient levels by 35 days (Table 1). However, as noted in the Discussion below, recovery dynamics following a similar, natural heat wave would be dependent on individuals present to reseed the community.

Native tunicates, including the solitary *Ascidia ceratodes* and colonial *Distaplia*, were less resistant than non-native bryozoans and recovered more slowly than non-native tunicates. Both *Ascidia* and *Distaplia* were negatively impacted by the heat wave (Table 1). Although *Ascidia* abundance was > 0% on average at all time points (Table 1), abundance was 0% on all heat-wave plates at either day 0 or day 5. *Ascidia* did not recover to ambient levels until the 95-day census (Table 1). Recovery of *Distaplia* was harder to assess, as cover on ambient plates also declined. However, initial cover on heat-wave plates was 14.7 ± 4.5%, and the heat wave resulted in 100% mortality during the experiment (for survival after the experiment, paired $t = 3.26$, $DF = 7$, $p = 0.014$). In the heat-wave treatment, *Distaplia* represented only 1% cover on a single replicate (out of $n = 8$ plates) at 35 days, and no *Distaplia* were found on these plates at 95 days (Table 1).

Field plates

On average, recruitment declined over the 95-day experimental period (slope $t = 18.5$, $DF = 3$, $p < 0.001$, Fig. 4a), with this pattern driven largely by the invasive tunicate *Diplosoma*. Despite its failure to recruit to heat-wave plates (Table 1), *Distaplia* recruited in high abundance (numbers greater than 6–7 of the other species) both early in the recovery period and in October and November (Fig. 4a). *Ascidia* was only found on a single recruitment plate during the study, but it did recruit to field control plates suggesting that its recruitment is patchy and may be better estimated with longer recruitment sampling intervals (Fig. 4).

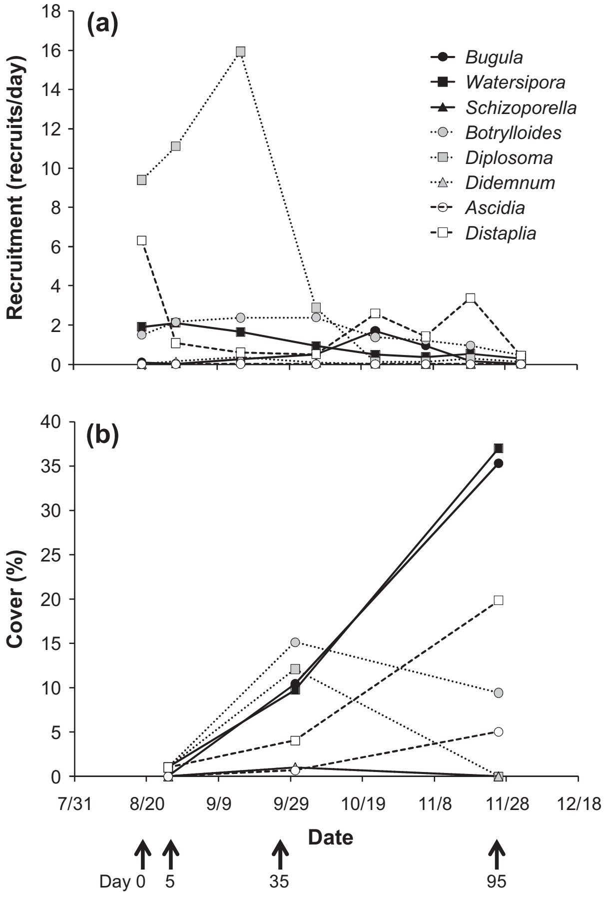

Figure 4. Recruitment and community development on unmanipulated field plates. (a) Recruitment patterns of fouling species onto empty plates suspended from the dock adjacent to our experimental plates. Values represent the mean number of recruits per day that settled on 10 × 10 cm plates ($n = 4$), and dates represent the midpoint of each 1- to 3-week sampling interval. (b) Community development on empty 10 × 10 cm plates ($n = 3$) deployed concurrent with the lab experiment and censused at 5, 35, and 95 days. In both (a) and (b), variances are omitted for clarity.

Mean cover on field control plates increased over time (slope $t = 18.8$, $DF = 2$, $p = 0.003$, Fig. 4b). At 95 days, the most abundant species were the invasive bryozoans *Bugula* (35.0 ± 14.4%) and *Watersipora* (36.7 ± 19.6%) and the native tunicate *Distaplia* (19.7 ± 15.2%). *Ascidia* also settled and grew on these plates, though its distribution was very patchy; at 95 days, *Ascidia* represented <1%

of cover on 2 of 3 plates, but 15% cover (ranked 2nd after *Watersipora*) on the 3rd plate.

Invasive species richness was higher on heat-wave plates than on field plates (ANOVA $p = 0.019$ after Tukey adjustment for multiple comparisons) but did not differ between ambient-experimental and field-control plates (ANOVA $p = 0.358$ after Tukey adjustment). In contrast, native species richness was higher on ambient experimental plates than on field plates (ANOVA $p = 0.048$ after Tukey adjustment) but did not differ between heat-wave and field control plates (ANOVA $p = 0.932$ after Tukey adjustment).

Discussion

We show that heat waves, which are predicted to increase in frequency and severity with climate change, can significantly impact a marine community. The heat wave caused an overall decline in total species richness and cover. Even when richness and cover reached ambient levels (between 5–35 and 35–95 days of recovery, respectively), the proportion of species richness that was comprised of non-natives remained higher in the heat-wave treatment. The decline of native species was driven largely by the decrease of *Distaplia*; however, the community impact was only significant when considering the cumulative responses of all seven native species present on the plates (Supplementary material Appendix 1 Table A1). Invasive richness, on the other hand, initially declined in the heat-wave treatment but, by the 35 day census and through the duration of the experiment, heat-wave plates contained an average of one additional invasive species compared to ambient plates.

Based on our examination of the eight most common species on the adult plates, resistance to the heat wave appeared to be predicted by a combination of species' origin (native vs non-native), higher order taxonomy and morphology (MacGillivray et al. 1995; Table 1). The most resistant group was the non-native bryozoans. These species never declined, and two of them, *Bugula* and *Schizoporella*, capitalized on the newly available bare space and increased in abundance in the heat-wave treatment. In contrast, both non-native and native tunicates experienced almost 100% mortality following the heat wave.

Resistance to the heat wave also differed by age; however, contrary to expectations, juveniles were more resistant to the heat wave than adults. The only species that suffered greater juvenile mortality in the heat-wave treatment was the native *Distaplia*; survival of the six most common non-native bryozoan and tunicate species was unaffected by the heat wave (and resistance of juvenile *Ascidia* could not be assessed because none were present on juvenile plates). Despite an increase in mortality of the most common native species, there was no influence of the heat wave on richness or cover on the juvenile plates. Though a large body of literature supports a positive relationship between age and thermal tolerance (Gosselin and Qian 1997, Hunt and Scheibling 1997), a decrease in heat-wave resistance with age has also been shown for some insect species (Bowler and Terblanche 2008). We suggest that ontogenetic variation in temperature tolerance merits further study for marine invertebrates in the fouling community, since life-stage effects could further modify predictions of community responses to climate change.

Recovery and community development following the heat wave occurred via growth (of resistant individuals) and/or recruitment of new colonists (but see below for potential implications of a natural heat wave for this larval pool). Both growth and recruitment likely contributed to final abundances of the non-native bryozoans. When less resistant tunicates died and sloughed off of the plates following the heat treatment, skeletons that initially appeared dead and empty yielded live colonies of the encrusting bryozoans *Watersipora* and *Schizoporella*. In addition, *Bugula* and *Watersipora* (but not *Schizoporella*) were both recruiting during the recovery period and became the two most abundant species on the field control plates at 95 days. In contrast, for all tunicates, recovery was primarily through recruitment of juveniles into bare space, although some asexual growth may have occurred from colony fragments that were initially classified as dead. While propagules of both natives and non-natives were present (based on recruitment and field plate data), non-native individuals appeared to recruit and become established more readily to the bare space that had become available on the heat-wave treatment plates. The decrease in *Distaplia*, even on the ambient plates, does not appear to represent a seasonal decline per se, as *Distaplia* was the third most abundant species (representing ~20% cover) on the field control plates. This decline, thus, could be due to additional species interactions, such as interspecific competition on the ambient plates. At the same time as *Distaplia* was decreasing on the ambient plates – and failing to recover on the heat-wave plates – *Ascidia* was able to acquire enough space, through successful recruitment and establishment, so that native cover did not differ between heat-wave and ambient plates by 95 days.

Multiple lines of evidence suggest that we may have underestimated the impacts of such a heat wave by, rather, overestimating these species' ability to recover from a natural heat wave. This is because, if similar mortality rates occurred in the field, the reproductive adults responsible for reseeding the community would include only (1) resistant individuals, and (2) less- or un-affected individuals living in temperature refuges. For a heat wave of similar magnitude, the only resistant individuals would be (of our eight focus species) the three non-native bryozoans. For the highly susceptible species (those that experienced immediate and nearly complete mortality), recovery would depend on colonization of propagules produced by surviving individuals. In Bodega Harbor, one potential temperature refuge is habitats at greater depth. Interestingly, researchers SCUBA diving in Bodega Harbor have observed four of the six focal non-native species – *Botrylloides Bugula*, *Didemnum*, and *Diplosoma* – at depths of at least 5 m (and up to > 10 m for *Bugula*; J. Byrnes, K. Hultgren and F. Tomas pers. com.), suggesting the existence of local populations that could be less affected by such a heat wave and contribute to recolonization. Whereas we evaluated impacts of an increase in heat-wave severity, the predicted increases in heat-wave frequency and length are also both likely to exacerbate these impacts (Meehl and Tebaldi 2004). As heat waves become more frequent, species may be successively excluded when their recovery time (via growth or colonization from refuges) begins to exceed the time between consecutive heat waves. Furthermore, a heat wave of sufficient length and severity could cause widespread mortality of even the most resistant species instead of having the species-specific impacts of a medium-severity disturbance (Allison 2004). In this case, recovery would depend solely on new recruitment of propagules from unaffected (e.g. refuge or distant) populations.

Another factor that could accelerate a positive feedback between heat waves and non-native species is the projected increase in mean temperature. Warming ocean temperatures could affect recruitment patterns, recovery dynamics, and, as impacts accrue, pre-heat-wave species composition. For example, Stachowicz et al. (2002) found that increased winter temperatures were associated with earlier and greater total recruitment of non-native tunicates. In addition, higher temperatures are positively associated with growth rates of non-native species and negatively associated with survival of native species (Stachowicz et al. 2002, Sorte et al. 2010b). Thus, following a heat wave, non-native species are likely to be at an advantage over natives when overall mean temperatures are higher because non-natives may recruit earlier and in greater numbers, acquire space faster via growth, and maintain space better due to lower mortality rates. There is the potential that physiological acclimation could ameliorate impacts of climate change in these fouling species (Somero 2002). Adaptation is also possible, especially given the relatively low dispersal distances and short generation times in subtidal epifaunal communities (Boyd 1972, Osman and Whitlatch 1998), although this possibility is currently untested.

The proximal responses to heat waves discussed here for adult-dominated communities, which represent the majority of cover, have implications for several potential changes in community structure and dynamics. First, in systems such as the fouling community where space is a limiting resource, species turnover depends on disturbance events that create open space, and changes in disturbance regimes will impact community assembly (Connell 1978). If disturbance patterns – such as the frequency or timing of events – change, then communities will likely change, due to factors including seasonal differences in the number and types of propagules available to recolonize the disturbed area. In fouling communities, in particular, widespread mortality events and subsequent increases in bare space have primarily been observed in the winter and associated with low salinity events (Nydam and Stachowicz 2007). Importantly, since the identity and number of species recruiting varies seasonally, communities that develop in bare space created during the summer by future heat waves are likely to differ greatly from those developing in the wintertime. Second, heat waves may precipitate not just changes in species abundances but shifts in geographic distributions (Parmesan et al. 2000). For example, a recent study by Thibault and Brown (2008) followed the 'invasion' of the native pocket mice into adjacent areas facilitated by an extreme flood event that caused widespread mortality in the incumbent dominant kangaroo rat species, allowing pocket mice to colonize and establish territories. In addition, it has been suggested that the 2003 European heat wave may have facilitated the expansion of the Atlantic snake pipefish in the northeast Atlantic (Fleischer et al. 2007, Harris et al. 2007, Sorte et al. 2010a). Native species may also experience a range contraction following local extinction (Parmesan et al. 2000), especially if species are already more stressed at range boundaries (Sorte and Hofmann 2004). Third, shifts in species composition, especially with increases in invasive species, can lead to cascading negative impacts on other members of the community and increased economic costs (Carlton 2001). As an example, one of our study species, the relatively heat-wave resistant bryozoan *Watersipora*, has low susceptibility to predation, high resistance to anti-fouling paints, and a three-dimensional growth form that increases drag and, therefore, fuel costs (Floerl et al. 2004, Nydam and Stachowicz 2007).

In conclusion, our study shows that heat waves, which are observed and predicted consequences of historical and future climate change, can have significant impacts on the composition of a subtidal epibenthic community. In addition, our results highlight the potential for interactions between global warming and invasive species, which are, individually, two of the greatest threats to biological systems, and this interaction is likely to exacerbate their impacts. The impacts of warming and invasions on biodiversity can alter ecosystem functioning (Zavaleta and Hulvey 2007, Hawkins et al. 2009), especially given interactions between the effects of temperature and richness on ecosystem processes (Bulling et al. 2010). We also suggest that feedbacks will occur between responses to increases in extreme and mean temperatures since mean temperatures may increase the suitability of the environment for, and thus initial abundances of, non-natives relative to natives (Sorte et al. 2010b). Studies of species' and community responses to environmental extremes, which have been less well-studied than increases in mean temperature, are necessary in order to predict rapid biological changes in response to future extreme events.

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Supplementary material (available online as Appendix O18663 at www.oikos.ekol.lu.se/appendix. Appendix 1