RESEARCH ARTICLE

Water Temperature as a Limiting Factor in the Colonization of a Partially-Restored Coastal Lagoon: Case Study of a Gastropod Herbivore and Control of Macroalgae

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ABSTRACT

East Harbor (Truro, Massachusetts, U.S.A.) is a tidally-restricted salt marsh lagoon that has undergone partial restoration since 2002. After reintroducing seawater to the system following nearly 140 years of impoundment, remarkable transformations in plant and animal communities have occurred. But while a host of marine fish, crustaceans, and benthic invertebrates have become established throughout the system, an important herbivore, common periwinkle (*Littorina littorea*) has not. This gastropod is absent throughout the open lagoon where in the past several years macroalgae (mainly *Enteromorpha intestinalis*) has proliferated to nuisance levels. Grazing experiments with common periwinkles suggest that this species could significantly reduce the extent of macroalgae biomass there. The inability of this organism to colonize the lagoon may be related to high water temperatures. Laboratory experiments suggest that 4 days of constant water temperatures ≥ 28°C or 6+ daily hours of 30°C for several days result in high mortality. Data from *in situ* temperature loggers show that such conditions occur in the lagoon during July–August. Increased tidal flushing could lower water temperatures throughout East Harbor and allow this species to expand its range. This, in turn, could limit the development of macroalgae through herbivory. This study highlights the role of keystone species and the importance of restoring suitable temperature regimes for the functional recovery of hydrologically-impaired systems.

Keywords: Cape Cod, *Littorina littorea*, macroalgae, periwinkle, salt marsh, temperature, tidal restoration

Coastal ecosystem restoration projects tend to be highly variable in terms of their process of recovery and the extent to which they ultimately resemble reference sites (Zedler 2000, 2001). Rates of recolonization of both plants and animals may occur at vastly different spatial and temporal scales. As such, there may be periods of time during recovery when certain keystone species are either overly abundant or absent from the system. Such imbalances can have profound ecological effects, and there are many examples of this from terrestrial, aquatic, and marine ecosystems (Mills et al. 1993 and references therein). Keystone species relevant to coastal habitats include oysters (Brumbaugh et al. 2000), eelgrass (Bernard et al. 2005), fiddler crabs (Smith et al. 2009), purple marsh crabs (Holdredge et al. 2009), snails (Kinlan et al. 1997), and a variety of other vertebrate and invertebrate organisms, depending on the system. When none or very few of these important species become established in a ecosystem undergoing restoration, there may be considerable setbacks in terms of restoring ecological function.

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East Harbor (Truro, MA, U.S.A.) is a former salt marsh lagoon within Cape Cod National Seashore (CCNS) that has undergone partial tidal restoration. Since the opening of clapper valves in a long drainage pipe (2002) that used to prevent seawater from entering the system, a wide variety of estuarine organisms have colonized and proliferated within the lagoon (Portnoy et al. 2008, Thelan and Thiet 2008). In 2005, however, increased macroalgal growth was also noted, and in 2006–2007 macroalgae biomass (particularly *Ulva intestinalis*) was very high. This caused a number of problems, including the smothering of seagrass beds and widespread shellfish die-offs (Portnoy et al. 2008). Today, macroalgae remains the dominant form of plant life in the lagoon and is believed to be inhibiting the recovery of seagrasses and various benthic fauna.

Common periwinkle (*Littorina littorea*) is a voracious consumer of macroalgae but has failed to colonize East Harbor. This organism has long been naturalized to North America and is a common resident of salt marshes and

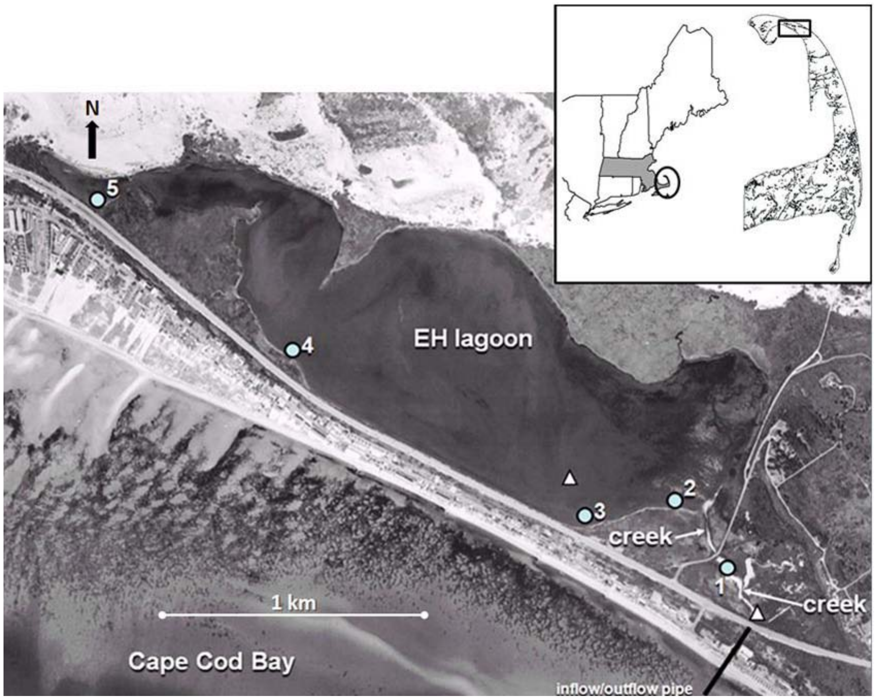

Figure 1. Map of East Harbor system with grazing bioassay (circles) and YSI logging locations (triangles). Upper right diagrams show the location of Cape Cod (circle) within the Commonwealth of Massachusetts (shaded) and the location of East Harbor (square) on the Cape Cod peninsula.

estuaries in Canada and the northeastern United States. It feeds on many different types of macroalgae, particularly ephemeral greens such as *Ulva* spp. (Bertness 1984, Norton et al. 1990, Wihelrnsen and Reise 1994, Lotze and Worm 2000, Lotze and Worm 2002, Korpinen and Jormalainen 2008). As such, common periwinkle is considered a keystone species in the functioning of marine and estuarine ecosystems (Lauckner 1987, Morin 1999). Shortly after tidal exchange was initiated at East Harbor, common periwinkles were observed within the main tidal creek, which winds through an emergent marsh and is the sole connection between Cape Cod Bay and the open lagoon (Figure 1). However, in the lagoon itself, common periwinkles are extremely rare or, in more recent years, totally absent (Portnoy et al. 2007, Thelan and Thiet 2008).

The question, then, is: why hasn't common periwinkle expanded its distribution into the lagoon? Abiotic factors such as salinity, dissolved oxygen, water flow, and substrate (e.g., peat banks, cobble, riprap) availability are highly suitable (Fischer 1948, Rosenberg and Rosenberg 1973, Lauckner 1984, Wahl and Sonnichsen 1992, Pannunzio and Storey 1998, MacDonald and Storey 1999, Sokolova 2000, Greenway and Storey 2001, De Wolf et al. 2001a,b, Larade and Storey 2002, Saranchova et al. 2007, Larade and Storey 2009). Food (micro- and macroalgae) is abundant, and predators are scarce or absent from the lagoon (Thelan and Thiet 2008). Thus, the field of potentially limiting variables is small but includes one that is universally important in the biological functioning of ecosystems—temperature.

Common periwinkle is extremely cold tolerant and can withstand temperatures well below freezing, as its range in North America extends north to Labrador, Canada. However, summer water temperatures in East Harbor can approach or exceed 30°C (Portnoy et al. 2008). Although heat tolerance in common periwinkles may vary geographically among populations (Clarke et al. 2000b), water temperatures > 30°C have been reported to induce significant mortality in this species (Newell et al. 1971, Hamby 1975). Thus, high temperatures in this shallow (1–2 m depth), still poorly-flushed, lagoon may be a key factor preventing periwinkles from establishing there.

The absence of an herbivore that can exert considerable top-down control of macroalgae is a potentially critical factor in this system's response to partial restoration of tidal flow. The main objectives of this study were to determine whether common periwinkles, if present in the lagoon, could significantly reduce the growth of macroalgae and, secondarily, whether temperature may be limiting their establishment. To do this, we evaluated the ability of transplanted common periwinkles to graze macroalgae in the lagoon and documented their survival, experimentally assessed the heat tolerance limits of the common periwinkle population currently residing in the tidal creek (i.e., the local genotype), and analyzed 8 years of temperature data from the creek and lagoon.

Methods

Site Description

East Harbor is a ~140-ha open water back barrier lagoon surrounded by a similar area of peripheral marsh. In the mid-1800s, the natural inlet to East Harbor (~300 m wide) was filled, and the system was cut off from tidal exchange with Cape Cod Bay. In 2002, CCNS and the town of Truro undertook partial tidal restoration using a 1.2-m diameter drainage pipe built in the 1930s to allow discharges into Cape Cod Bay when water levels were high. Several 1-way flapper valves in the pipe were fixed in an open position which has facilitated a limited amount of seawater exchange. Tidal flows range between 1.82–2.51 m^3/s on flood tides and between 1.18–1.48 m^3/s on ebb tides (Spaulding and Grilli 2005).

Grazing Bioassays

We conducted macroalgae grazing experiments in the spring and summer of 2008 at 5 sites ranging from the tidal creek to the NW cove (Figure 1). We ran 3 assays from May 15–June 23, June 23—July 16, and July 16–August 19. At each site, we placed periwinkle enclosures (cages) on the sandy bottom a few meters away from the shoreline in ~ 30 cm of water. The cages were circular rings approximately 20 cm high constructed out of hardware cloth with the upper edge bent 90 degrees to form an inward-facing "lip". The cages were pushed into the sediment to a depth of ~ 5 cm to prevent periwinkles from going under and out (although common periwinkles are epifaunal and do not burrow). No tops were put on the cages because they would be quickly fouled with algae, which would result in severe shading of everything below, thereby altering water temperature and macroalgal growth inside the enclosures. The short walls of the containers were fouled only to a small extent during the study period, and we used a scrub brush to remove any fouling algae on a regular basis. We used a total of 9 cages (3 per treatment) per site. Within each cage, we inserted 3 sections of PVC pipe (3.2-cm diameter) into the bottom so that 20 cm protruded from the sediment surface, thus providing a known area of substrate (~600 cm^2) on which algae could grow (Figure 2).

Treatments consisted of high density (H = 20 periwinkles per enclosure; equivalent to 100 periwinkles/m^2), low density (L = 10 periwinkles per enclosure; equivalent to 50 periwinkles/m^2), and controls (C = no periwinkles). Natural abundances of common periwinkles can be highly variable, but the high density treatment described above is generally lower than the mean value recorded for salt marshes of southern Maine (Tyrrell et al. 2008), and densities > 1,000/m^2 have been recorded (Saier 2000, Buschbaum 2001).

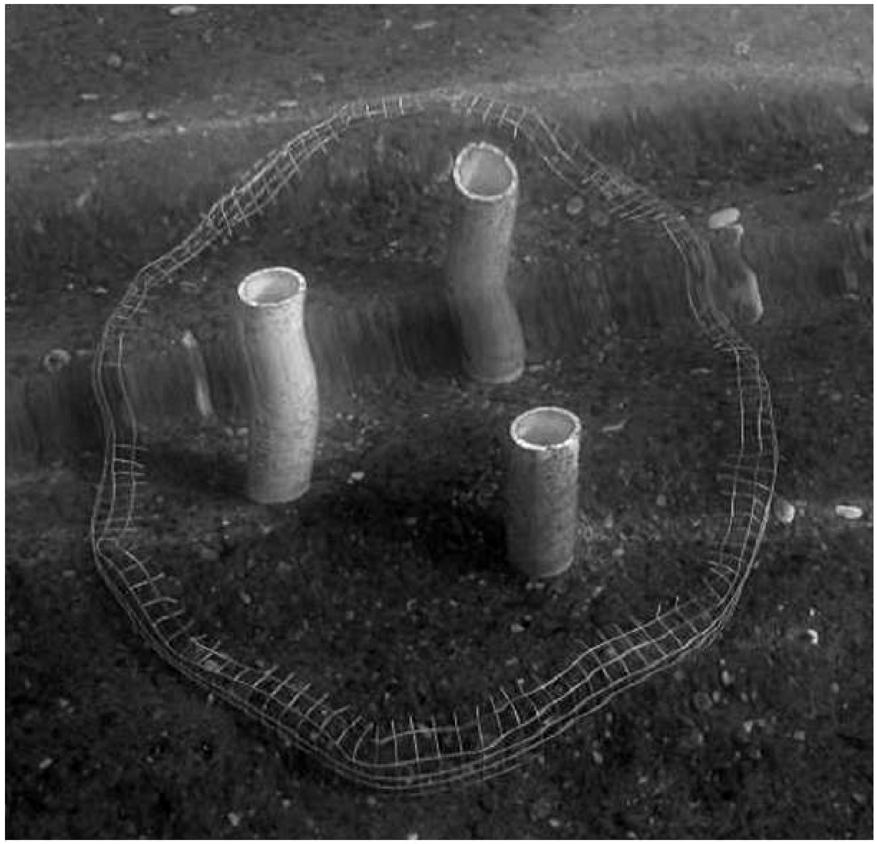

Figure 2. Photo showing the design of a cage with PVC substrate.

After ~ 1 month, we collected all algae (both macroalgae and microperiphyton) that had grown on the PVC substrate by scraping it off and placing it in Ziploc® bags. We then immediately reinserted the PVC into the sediment. We brought the samples back to the laboratory where the dominant species of algae were identified. Subsequently, we dried and weighed the entire mass of algae in each sample at 80°.

Periwinkle Mortality in the Field

Although our original intent was to document periwinkle survival at regular intervals throughout the course of the entire study, many individuals were difficult to find unless they were actively grazing on the PVC. Accordingly, we harvested and evaluated the periwinkles just once at the end of the last assay period (August 20). At this time, we assessed periwinkle mortality based on well-established criteria (Hamby 1975, Clarke et al. 2000a).

Periwinkle Mortality in the Lab

To get an idea of expected or "normal" mortality rates for the East Harbor creek common periwinkle population living in non-stressful conditions, we filled 6 containers (28L × 20W × 18H cm) with lagoon water at the North Atlantic Coastal Laboratory (CCNS, Truro, MA). We then placed 10 periwinkles collected from the creek in each container. Water temperature was maintained at ~ 20°C, and all containers were supplied with light, aeration and the same species of macroalgae that grew on the PVC pipes in the field (*Ulva lactuca*, *E. intestinalis*, and *Neosiphonia harveyi*). We changed the water every 2 weeks. We documented periwinkle survival over the course of 3 months (October 1, 2009–February 1, 2010)—1 month longer than they were monitored in the lagoon during the summer of 2008.

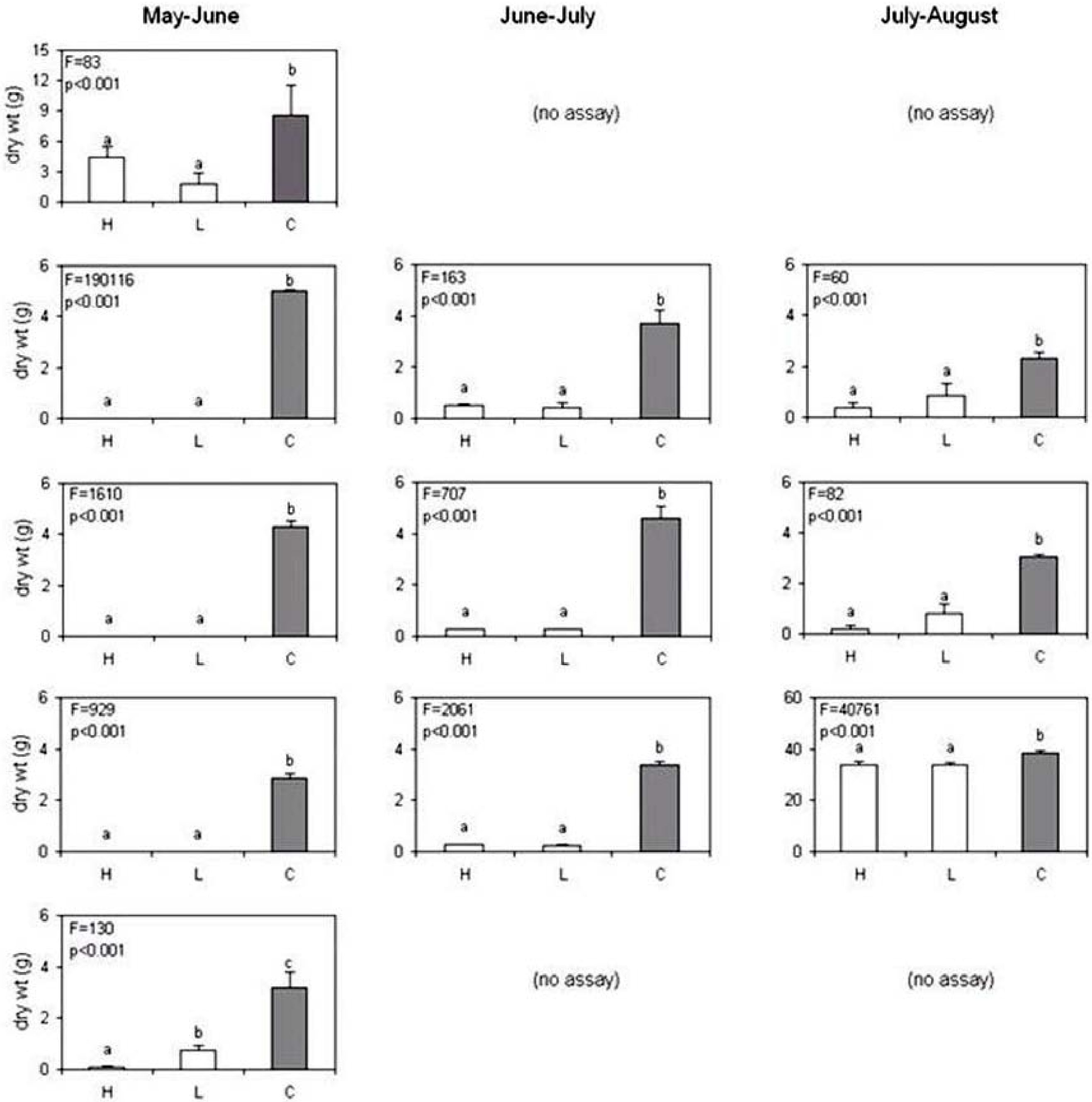

Figure 3. Dry weights of algae (macroalgae and microperiphyton) harvested from the PVC by treatment, assay period, and site (open bars = cages with common periwinkle, shaded bars = control groups; different letters denote statistically significant differences as determined by Tukey's HSD tests; F and *p* values are from one-way ANOVAs run on each individual assay for treatment effects, α = 0.05).

Heat Tolerance Bioassays

We conducted heat tolerance bioassays under carefully controlled laboratory conditions in 2009 in order to assess how periwinkle fitness was influenced by temperature. Prior to each assay, we collected common periwinkles between 10–15 mm (shell height) from the resident population in East Harbor's main tidal creek and brought them back to the laboratory. We then subjected periwinkles to different levels of constant temperature or variable temperatures.

Water temperature was controlled in each container using Stealth™ aquarium heaters (Marineland Aquarium products, Cincinnati, OH). Constant temperature (CT) assays consisted of water kept at 22, 23, 25, 27, 28, and 30°C. We ran a total of 5 CT bioassays between July 14 and August 13 2009. New assays were begun as soon as 100% mortality was reached in a treatment group. For the variable temperature assays, the heaters were connected to timers which turned on the units (pre-set to specific temperatures) for 0, 6, 12, and 20 hrs at 30°C. This temperature was chosen based on literature values for heat coma induction (Hamby

1975) and data from previous years showing that maximum 6- to 20-hr average temperatures either exceed or approach 30°C. For both constant and variable temperature (VT) bioassays, we monitored the water in each container regularly using hand-held thermometers. Treatments with no heating (i.e., 0 hrs) remained near 23°C. We ran a total of 5 VT bioassays between August 25 and September 8. We collected new periwinkles from the tidal creek for each assay (i.e., the same ten were not used for each separate assay run). All were kept in clear plastic containers (28L × 20W × 18H cm) (5 individuals per tub) filled with fresh seawater collected from East Harbor (25–30 ppt salinity). We provided continuous aeration, light, and food (*U. lactuca*) to ensure that all other living conditions were suitable.

In Situ Temperature Logging

As part of CCNS's long term hydrologic monitoring program for tidal restoration projects, YSI™ data-loggers (Yellow Springs, Ohio) were deployed in East Harbor within the tidal creek in 2004, 2007, 2008, and 2009 and in the lagoon near the SE shoreline from 2003–2009 (see Figure 1 for locations). All data except those from 2005 and 2008 were collected from June through mid-September. Data from 2005 were only collected from August 11 to September 30; 2008 creek data from June 22 to August 27. The units were positioned so that the temperature sensors were located midway between the bottom and the water surface (~50 cm from the bottom in the lagoon and 75cm in the creek). Water depth was generally between 1 and 2 m at the lagoon site and between 1 and 1.5 m at the creek site due to tidal fluctuation there. Temperatures were recorded every 30 min. Salinity and percent dissolved oxygen (DO) data were also collected by the lagoon unit every year except 2005, and from the creek in 2007–2009.

Statistical Analysis

We log-transformed algae dry weight values from the field grazing experiments to improve normality and homogeneity of variances. We subjected the data (all sites, all assay periods) to factorial ANOVA (Statistica™ ver. 7.5) to test for overall individual and interactive effects of time, site, and treatment. In addition, we used one-way ANOVA and Tukey's HSD tests in our analyses of treatment effects in each monthly assay. We arcsine-transformed percent mortality values in the laboratory thermal tolerance bioassays and subjected them to one-way ANOVA. We compared specific treatment means using Tukey's HSD tests (α=0.05). We calculated maximum water temperature averages for various time periods from the YSI data in order to assess both short (6 hr) and longer term (12 hr, 20 hr, 4 d) peaks in water temperature in the lagoon and creek.

Results

Effect of Periwinkles on Macroalgae Growth in the Field

At site 1 (in the creek), algae drifting back and forth in the tidal currents became a problem. The PVC pipes were frequently inundated with large masses of algae that had not originated on them, but had simply become entangled. These clumps had to be removed on an almost daily basis throughout the duration of the assay. At site 5, there was so much macroalgal growth in the experimental area that it soon became difficult to even find the cages. Because of these logistical problems, only sites 2, 3, and 4 were used in the June–July and July–August assays.

Time of assay ($F = 530.8$; $p<0.001$), site ($F = 396.3$; $p <0.001$), and treatment ($F = 675.4$; $p <0.001$) all had significant effects on the biomass of macroalgae and attached microalgae (hereafter termed microperiphyton) and all interactions were significant (time*site $F = 502.5$, $p<0.001$; time*treatment $F = 40.8$, $p<0.001$; site*treatment $F = 11.1$, $p<0.001$; time*site*treatment $F = 3.7$, $p = 0.002$). Periwinkle effects were consistent across all sites and during all assays. Algal biomass was very high in the control treatments and extremely low to nonexistent in both high- and low-density periwinkle treatments, which rarely differed from each other (Figure 3). In fact, almost no algae (< 0.01 g) of any kind could be scraped from the PVC in cages with periwinkles at sites 2, 3, and 4 in the May–June assay. Algal biomass in the control treatments at these sites ranged between 2.30 g (site 2, July–August) and 5.01 g (site 2, May–June). The one anomaly was site 4 during the July–August bioassay, where *N. harveyi*/*Cladophora albida* was abundant in all 3 treatments. Despite the prolific growth, however, algae biomass in the H and L groups was still significantly lower than in the C treatment at this site.

The macroalgae species that grew on the PVC were the same types identified in Portnoy and others (2007) on natural substrates within the lagoon, but there were differences in the dominant species of algae among sites and over the course of the study. Examination of control cages, where there was no confounding effect of snail grazing, revealed seasonal shifts. In May–June, *U. intestinalis* was dominant at sites 1, 2 and 5, while microperiphyton dominated at sites 3 and 4. Microperiphyton continued to dominate at site 3 in both June–July and July–August. At site 4, the microperiphyton community gave way to *C. albida* in June–July and then a mixture of *N. harveyi* and *C. albida* in July–August. The H and L periwinkle treatments most often resulted in the attached algae being dominated by microperiphyton, which itself consisted mostly of pennate diatoms (not identified to species), since constant grazing prevented larger macroalgae from becoming established.

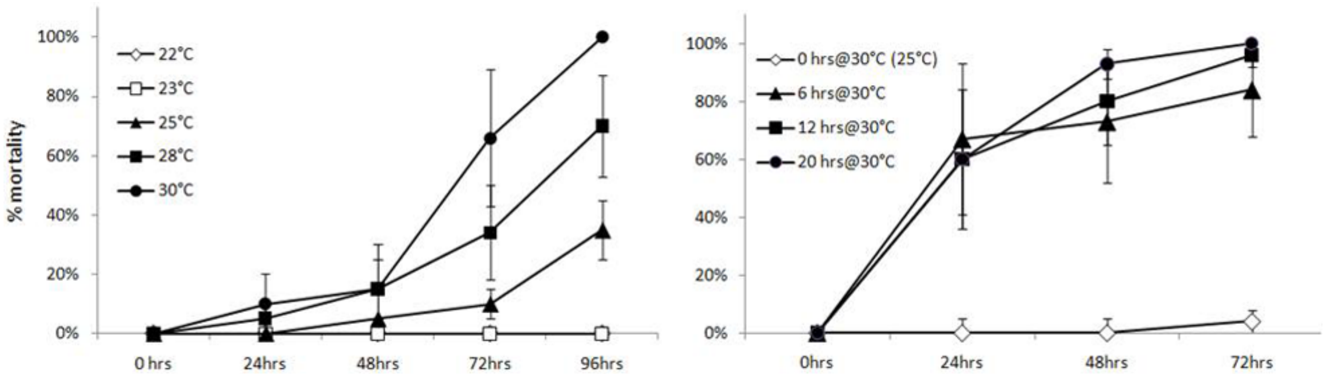

Figure 4. Percent mortality in constant (left) and variable (right) temperature treatments. Values are means of 5 assays. Treatments with the same letter are statistically indistinguishable; those with different letters are significantly different (error bars are standard errors of the means).

Periwinkle Survival

Anecdotally, it appeared that very little mortality occurred until the July–August assay (they were collected on August 20). Although the final number of periwinkles recovered at the end of the study varied (some were missing and recovery ranged between 78% and 86%), very few that were originally introduced to each site (n = 90) were found alive. In addition, there were large differences in periwinkle mortality among sites. At the westernmost site, 70% mortality was recorded among 75 individuals found. Further east at sites 3 and 2, mortality was 45% (n=66) and 36% (n=70), respectively. Periwinkles kept for 4 months in East Harbor seawater in the laboratory at ~20°C exhibited 100% survival in all containers.

Heat Tolerance Bioassays

Even slight differences in constant temperature regime had significant effects upon periwinkle survival (F = 16.5, $p<0.001$; Figure 4). Constant temperatures of 28°C and 30°C resulted in 70% and 100% mortality within 96 hrs, respectively, whereas temperatures of 22°C and 23°C caused no mortality in any of the 5 assays. Curiously, 25°C resulted in greater mortality values than 27°C, but these treatments were statistically indistinguishable.

Variable temperature assays, which were conducted later in the summer, showed even more pronounced responses to high temperatures (F = 21.5, $p<0.001$). An average of 67% of periwinkles died after only 6 hrs of exposure to 30°C (Figure 4). After 72 hrs, the vast majority or all of the periwinkles were dead after varying lengths of exposure to 30°C. The control groups, which were maintained at room temperature of 23°C, showed almost no mortality.

In Situ Temperature Logging

Long term YSI data (2003–2009) on water temperature in the tidal creek vs. lagoon indicated differences between them. The tidal creek was consistently cooler during the periods of highest water temperatures (Table 1). For short-duration maximum averages (6 hrs), the 2 sites were relatively similar, which is logical since the water in the creek during ebb tide is essentially all lagoon water. However, the 12 and 20-hr maxima were much different—between 2–3°C cooler in the creek. Maxima for a 4-day period showed even greater disparity between the lagoon and creek. An interesting temporal trend in both the lagoon and creek is that temperatures increased by ~ 2°C between 2005 and 2006 and have stayed warm ever since.

Salinity in the lagoon ranged between 14 ppt (2003) and 30 ppt (2007), while salinity in the creek ranged from 16 ppt (2007) to 33 ppt (2007, 2008). Percent DO was highly variable, showing a large range of values for the creek and the lagoon in all years. Anoxic conditions (0% DO) occurred twice for a total of 3 hrs (2hrs, 45 min continuous) in 2003 and 8 times for a total of 8 hrs (only 2 hrs continuous) in 2004. Since 2004, however, % DO has not reached 0% at any time in either the creek or lagoon. In 2007–2009, % DO minimums were higher in the lagoon than the main tidal creek.

Discussion

Some periwinkles survived in the cages during the course of the summer in 2008. In hindsight we recognize that survival may have been enhanced by the ability of snails to crawl inside the PVC pipes into an environment which was dark and undoubtedly cooler. In addition, periwinkles in the field experiment were protected from desiccation and high air temps by containing them underwater. As such, they did not experience the stress that they normally do when exposed at low tide. Typically, this is a time during which they are inactive and do not feed.

The fact that all of the periwinkles were not recovered at the end of the study somewhat compromises our ability to interpret the field-experiment data. If we assume that all or most of the missing periwinkles died, % mortality would be higher than the values presented above. However, considering that periwinkles experienced no mortality over the course of 3 months when kept in East Harbor lagoon water at cool temperatures, the observed mortality rates in the field (between 36% and 70) indicate a much reduced level of fitness.

Despite these limitations, the results of this study suggest that if common periwinkles were able to become established in East Harbor's main lagoon, it could significantly limit macroalgal growth in the system. The extent of macroalgae control would depend upon population size and distribution, but even low densities of common periwinkles were able to greatly reduce biomass in most assays, regardless of the type of algae. Unfortunately, the ability for this species to expand into the lagoon appears to be highly compromised by the current temperature regime.

Other variables may act individually or synergistically with temperature to influence periwinkle fitness and ultimately limit population growth. For example, trematode infection can reduce heat tolerance (McDaniel 1969, Huxam et al. 2001). Yet the importance of temperature alone can be recognized by integrating the results of the laboratory survival experiment, field temperature logger data, and thermal tolerance experiments. Maximum 4-day averages of YSI temperatures were very near or exceeded 28°C every year since periwinkles were last observed in the lagoon in 2005. In the laboratory setting, such conditions resulted in 70% mortality after 4 days. Temperatures are frequently even higher in the shallower, nearshore waters where the most suitable substrate for common periwinkles exists. In fact, surface water temperatures of 35°C have been recorded at various times during the summer months using hand held thermometers (Smith, unpublished data). Given that 80% mortality occurred in the 6hr@30°C experimental treatments after only 3 days, it is likely that temperatures in the nearshore waters of the lagoon could significantly reduce periwinkle fitness or effectively kill them over the course of a summer. We consider these experimental results quite robust as the provision of light, food, and continuous aeration otherwise made for near-optimal conditions.

Table 1. Maximum 6-, 12-, 20-hr, and 4-d average temperatures (YSI) in the lagoon and creek from 2003-2009. Values exceeding the 28°C critical threshold determined from the thermal tolerance bioassays are highlighted; 2005 data only collected from August 11 to September 30; 2008 creek data only from June 22 to August 27.

	Lagoon				Creek			
Year	6hr	12hr	20hr	4d	6hr	12hr	20hr	4d
2003	27.5	27	26.5	25.9	—	—	—	—
2004	27.7	27.2	26.5	25.4	26.6	25.4	25.0	24.4
2005*	28.8	28.3	27.6	26.9	—	—	—	—
2006	30.1	29.2	28.5	28.1	—	—	—	—
2007	29.7	29.3	28.6	27.7	27.9	26.1	25.7	25.1
2008*	30.3	29.7	28.8	27.7	29.0	27.4	26.7	26.3
2009	29.0	28.5	28.3	27.6	29.1	27.6	27.1	26.6

Periwinkles used in the variable temperature bioassays seem to have been more heat-sensitive than those subjected to constant temperatures, perhaps because these experiments were run later in the summer. These individuals had already experienced high temperatures throughout the course of the summer before being used in the laboratory experiments. Repeated incursions of high temperatures are important; Clarke and colleagues (2000a) reported that the temperature required to induce heat coma, which can lead to death, decreases (to as low as ~23°C) with increasing number of previous heat comas. At the very minimum, frequent heat stress, even if followed by recovery, would progressively compromise periwinkle fitness (Fraenkel 1960).

An increase in water clarity in the East Harbor lagoon occurred between 2004 and 2006, which is thought to be due to extensive filtration of phytoplankton by the exploding shellfish population (mainly softshell clam, *Mya arenaria*). This may have been an important development with respect to common periwinkles, as the resulting increase in light penetration noticeably warmed the water. The transition from cooler conditions during 2003–2005 to warmer ones (by ~ 2°C) after 2006 (Table 1) coincides with the disappearance of common periwinkles after 2005. Inter-annual climate variability does not explain this sudden jump in water temperatures as maximum and average air temperatures for July and August have been very consistent from 2003 to 2009, with variances of 0.5°C and 0.2°C, respectively (data from the Provincetown airport (7 km distant) weather records available at www.weatherunderground.com).

If summer water temperatures were lower, common periwinkles might be able to expand from the creek into the lagoon. In doing so, they could exert greater top-down control on both microperiphyton and macroalgae there. This can happen only if tidal exchange is further increased, which would bring larger amounts of colder Cape Cod Bay water into the system. Hydrodynamic modeling conducted by Spaulding and Grilli (2005) shows that increasing the size of the inlet would greatly reduce the residence time. This would cool the lagoon and also reduce nutrient concentrations (by dilution and flushing), thereby resulting in more bottom-up control of macroalgae. Lower water temperatures may also benefit other important organisms, including shellfish like softshell clam and eastern oyster (*Mytilus edulus*), northern quahog (*Mercenaria mercenaria*), and eelgrass (*Zostera marina*), which also suffer from thermal stress approaching or around 30°C (Kennedy and Mihursky 1971, Marsh et al. 1986, Grizzle et al. 2001, Bintz et al. 2003, Moore and Jarvis 2008, Jones et al. 2009).

Applicability to the Science and Management of Coastal Restoration

In general, this study illustrates the importance of temperature and the thermal tolerance ranges of organisms during ecological restoration. Temperature is routinely measured as part of a standard suite of water quality parameters, but there is often little or no discussion of its ecological meaning and cascading effects in predictions or analyses of ecosystem responses to restoration. This study further shows that the restoration of salinity by increasing tidal flow is not necessarily accompanied by temperature restoration. Shallow lagoons or coastal salt ponds with narrow tidal inlets may be particularly susceptible to this incongruence between salinity and temperature during restoration. In this regard, East Harbor may be analogous to certain southern estuaries where periwinkles are reportedly constrained to the tidal inlet areas where cooler waters prevail (Wells 1965 and references therein).

From a broader perspective, the results are a good example of how responses to tidal restoration can be highly variable and how ecological structure is precarious as plants and animals recolonize at different rates. Scientists and managers worldwide have recognized the importance of keystone species (and the creation of suitable habitats for them) in the restoration of rivers, and freshwater and coastal wetlands (Zedler 2000, Nienhuis et al. 2002, Elliott et al. 2007, Palmer 2008, Sanjeeva Raj 2008). Without full tidal restoration to cool the waters of East Harbor's lagoon, the prospect of achieving ecological balance will remain diminished because conditions for a key herbivore, common periwinkle, and other important species, may never develop.

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