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TITLE: Air temperature and winter mortality: implications for the persistence of the invasive mussel, *Perna viridis* in the intertidal zone of the south-eastern United States

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Abstract

Global climate change and invasive species represent two of the biggest threats to the environment. Biological communities are responding to global climate change through poleward shifts in distribution, and changes in abundance and phenology of both native and non-native species. An increase in the frequency and magnitude of extreme weather events is predicted with global climate change. Much is known about mortality events of marine organisms in relation to warm thermal stress with relatively little known about cold thermal stress, particularly in the tropics. Intertidal species are particularly susceptible to fluctuations in aerial conditions and many are considered indicators of climate change. *Perna viridis* is a recent invader to the United States where it fouls hard substrates and soft sediment habitats. During winter 2007-2008, a mortality event was observed for *P. viridis* across Tampa Bay, Florida. This mortality event coincided with extreme weather conditions when air temperatures dropped below 2°C for a period of 6 hours during low water. The minimum air temperature recorded was 0.53°C. During this period water temperature remained relatively constant (~20°C). We provide strong evidence supporting the hypothesis that thermal stress relating to exposure to cold air temperatures during emersion was the primary factor underpinning the mortality event. Similar mortality events occurred in 2009 and 2010, also coinciding with prolonged exposure to low air temperatures.

In the short term, weather may be responsible for the temporary trimming back of populations at the edge of their geographic but in the longer-term, it is expected that climate warming will trigger the poleward movement of both native and non-native species potentially facilitating biotic homogenisation of marine communities. The challenge now is to devise adaptive management strategies in order to mitigate any potential negative impacts to native biodiversity.

1. Introduction

Global climate change and invasive non-native species represent two of the most serious global threats to biodiversity and the environment (Stachowicz et al., 2002; Ward and Masters 2007). Biological communities are responding to global climate change through poleward shifts in distribution, and changes in abundance and phenology (Sims et al., 2004; Mieszkowska et al., 2005; Hiddink and ter Hofstede, 2008; Moore et al., 2010; Aprahamian et al., 2010; Wethey et al., 2011). Changes in distribution and associated species interactions have the potential to greatly affect the structure and functioning of communities (Moore et al., 2007; Firth et al., 2009). Climate change not only facilitates a shift in the distribution of indigenous species but also the establishment and extension in range of non-indigenous species (Stachowicz et al., 2002; Sorte et al., 2010a, b).

Furthermore, global climate change is expected to lead to an increase in the frequency and magnitude of extreme weather events (IPCC, 2007). Fluctuation in temperature is well documented as a driver of mortality in many marine species at temperate and subpolar latitudes (Orton, 1933; Harley et al., 2006; Coma et al., 2009; Firth and Williams, 2009; Sorte et al., 2011) and disease outbreak is often associated with increased temperatures (Harvell et al., 1999; Bruno et al., 2007). Conversely, mortality events driven by cold thermal stress have received less attention, particularly at subtropical and tropical latitudes; with the majority of studies describing effects on coral reefs in tropical waters (e.g. Laboy-Nieves et al., 2001; Saxby et al., 2003).

The record-breaking cold temperatures experienced in the Northern Hemisphere during winter 2009/2010 were a result of extremely negative values of the North Atlantic Oscillation (NAO) index (Wang et al., 2010). If the trend of increased frequency of NAO-negative years continues, it is predicted that more frequent cold outbreaks are likely in the future (Wang et al., 2010).

Prolonged cold outbreaks can have a severe detrimental effect on marine organisms, particularly those occurring in the intertidal zone (Crisp 1964; Wethey et al., 2011). Organisms living in the intertidal zone are of marine origin but experience terrestrial conditions daily during low tide. The upper distributional limits of intertidal organisms are set by physical factors such as thermal and desiccation stress (Connell, 1972; Somero, 2002; Harley et al., 2006; Hawkins et al., 2008, 2009). This vulnerability to terrestrial conditions infers that variations in climatic conditions are likely to elicit strong responses in intertidal organisms and result in changes in distribution and community structure and functioning (Fields et al., 1993; Lubchenco et al., 1993; Helmuth et al., 2006). The responses of intertidal organisms to environmental conditions has allowed for them to serve as proxies for changes occurring offshore (Mieszkowska et al., 2005).

The Asian green mussel, *Perna viridis,* is native to the tropical Indo-Pacific region, primarily distributed along the Indian and southeast Asian coasts (Siddall, 1980; Vakily, 1989; Rajagopal et al., 2006). This species was first recorded in North America in 1999, where it was found to be fouling the intake tunnels of a power station in Tampa Bay, Florida (Benson et al., 2001), and is thought to have been introduced through ballast water exchange (Power et al., 2004). The mussel has since spread to both the Gulf and Atlantic coasts of Florida (Ingrao et al., 2001; Baker et al., 2007) occurring as far eastwards as Panama City on the Florida Panhandle and north towards Georgia (Power et al., 2004). A recent survey indicated that individuals have extended as far north as South Carolina (Benson, 2010). The mussel is found attached to the many forms of hard structure introduced by man (pilings, docks, bridge supports) as the natural coastline is characterized by soft sediments. It occurs on these hard substrates both in the intertidal and in the subtidal zones, where it is also known to occur on soft sediments and among sea grass beds (Bell, pers. obs). Little is known about the impact of this species on native biodiversity but as its range expands, new interactions with indigenous species are likely to occur. For example, one observation suggests that *P. viridis* may out-compete the commercially important native eastern oyster, *Crassostrea virginica.* During a survey of *P. viridis* in Tampa Bay, Baker et al., (2007) observed a layer of dead *C. virginica* shells covered by *P. viridis.* Where living *C. virginica* was found, individuals were limited to the upper few centimetres of the intertidal, above *P. viridis*. Subsequent to a *P. viridis* winter die-off in January 2003, Baker et al., (2007) were unable to find any living *C. virginica* in the area previously occupied by *P. viridis.* It is well documented that mussels provide refuge and habitat for a wide variety of associated organisms (Seed, 1996) and that this function can vary with size of mussels (O'Connor and Crowe, 2007). Little is known about the biodiversity associated with *P. viridis* patches, but due to differences in size of individuals and patch complexity between oysters and mussels, it is likely that expansion of the green mussel will have potentially long-term effects on diversity of epibiota and mobile fauna.

While ecological information on the green mussel is quite limited after its spread to Tampa Bay, field observations at a small number of locations suggested that cold winter temperatures might be responsible for an observed temporary disappearance of *P. viridis* populations from the intertidal zone in Tampa Bay (Baker et al., 2007). Here, we examine data from a bay-wide survey of mussels to evaluate whether patterns of mussel distribution and abundance are suggestive of a large-scale mortality event. Likewise, by following mussels over a smaller number of sites for a 2-year period, we determine whether mortality events can potentially happen whenever acute cold weather events occur in Tampa Bay.

2. Materials & methods

2.1 Study sites

Tampa Bay, Florida exhibits an increasing salinity gradient from north to south (Barber et al., 2005). Nine survey locations were selected across a wide area of Tampa Bay, for which salinity data were available for the 12 months prior to December 2007, and comprised hard substrata (bridge pilings, pier pilings or pontoons) for attachment of mussels. Locations (Figure 1) that were surveyed were Safety Harbor Pier; McKay Bay Bridge; Ballast Point Pier; Gandy Bridge; Davis Islands Slipway; Fantasy Island Pier; Picnic Island Pier; Sunshine Skyway Bridge and Fort De Soto Slipway.

At each location, 12 quadrats (20 × 20 cm) were placed 1 m below the mean high water mark on all orientations of pilings or just below the water mark on pontoons. All mussels within quadrats were destructively sampled and measured (anterior to posterior) to the nearest 1 mm in the laboratory. The survey was initially carried out between 10-14th December 2007 in order to establish baseline information on the distribution and abundance of *P. viridis* in Tampa Bay. On a subsequent visit to Davis Islands in January 2008, it was observed that all of the mussels at the study site and surrounding area were dead. Following this, a complete resurvey of all locations was carried out from 18-20th February 2008 when it was suspected that a mortality event had occurred across Tampa Bay. All locations were again resurveyed from 5-6th May 2008. Individual mussels were categorised into size classes based on their antero-postero length: small (<49 mm); medium (50-99 mm); and large (>50 mm). In addition, the presence/absence of mussels was noted in the intertidal zone in summer and winter months at three sites: Courtney Campbell Causeway (near Safety Harbor), Gandy Bridge and Sunshine Skyway Bridge from 2008-2010.

2.2 Physico-chemical parameters

The Environmental Protection Commission of Hillsborough County collected monthly salinity (ppt) measurements by placing a probe just below the surface of the water at all sampling locations across Tampa Bay between January-December 2007. Additionally, data on air and water temperature on a 6 hour basis was obtained from a meteorological station near St. Petersburg Florida and supplied by TB-PORTS (Tampa Bay Physical Oceanographic Real-Time System) for all dates from 2007-2010 (Table 1).

2.3 Analyses

Analysis of variance (ANOVA) was used to test the *a posteriori* hypothesis that a mortality event occurred in Tampa Bay using density of mussels as the dependent variable. Two-factor ANOVA was performed using the factors: survey (3 levels, random, orthogonal); and location (9 levels, random, orthogonal) with 12 replicates. GMAV® version 5 for Windows was used for computations (Underwood and Chapman, 1998). Cochran’s test was used to test for heterogeneity of variances and Student–Newman–Keuls (SNK) procedure was used to make *post hoc* comparisons among levels of significant terms. Variances were heterogeneous, but it was not possible to transform the data.

One-factor ANOVA was used to test differences in salinity between sites using data from each month as a replicate (January-December 2007, n = 12). The relationship between mussel abundance and salinity was tested using least squares linear regression analysis (Sokal and Rohlf 2003).

3. Results

3.1 Mussel survey

324 quadrats were sampled comprising a total of 1452 mussels. Total mussel abundance (across 3 surveys) was highest at Safety Harbor (376) and lowest at Sunshine Skyway Bridge (23). Mean density per quadrat during the first sampling period (10-14th December 2007) was also highest at Safety Harbor (31.3), then Ballast Point (24.6) and lowest at Sunshine Skyway (1.91) and Fort De Soto (1.0) with other locations characterised by populations of intermediate density (Figure 2).

A bay-wide mortality event of *Perna viridis* occurred between December 2007 and May 2008 (Figure 2). On the second sampling period in February 2008, live mussels were only recorded at Gandy Bridge, Picnic Island and Fort De Soto (Table 2, Figure 2). At locations where no live mussels were observed within the quadrats, a broad visual search was done of the sampling site for any live mussels but none were recorded. Dead mussel shells were observed attached to the substrate or on the sea-bottom at many of the locations, indicating recent mortality. On the third sampling period (May 2008), populations at both Gandy Bridge and Picnic Island had also decreased to zero with Fort De Soto being the only location where any live mussels were recorded (Figure 2).

Surveys in 2009-2010 also indicated the disappearance of mussels after unusually cold temperatures. While mussels were present in October 2008 and 2009, none were found in January 2009 or 2010 on structures in the intertidal zone at the study sites.

3.2 Temperature data

The mean daily variation in air and water temperature for St. Petersburg, located within the middle reaches of Tampa Bay was recorded for the period between 11/12/2007 and 19/02/2008 (Figure 3). Water temperature was relatively constant, remaining above 20°C (20-25) for the majority of the period. Water temperature twice dipped slightly below 20°C (17-19) between 4-11th January and again between 16th January and 3rd February.

Air temperature was generally a few degrees cooler than water temperature (Figure 3), but a major drop in air temperature occurred between 2-4 January 2008 when temperatures remained below 15°C for 64 hours. During this 3-day period, the temperature dropped again and mussels were exposed to severely cold air temperatures (<2°C) for 6 hours when a minimum temperature of 0.53°C was recorded at 12:00 during low water (Figure 4).

Winter temperatures from 2009-2010 again showed a series of dates when air temperatures were less than 15°C. As in January 2008, air temperatures declined to near 0°C once and remained lower than 15°C for at least 3 days (Table 1).

3.3 Mussel abundance in relation to salinity

To characterise the relationship between mussel abundance and salinity, mussel abundance data collected during the 1st survey in December 2007 were considered in relation to the salinity data collected over the preceding 12 months between January-December 2007.

ANOVA revealed significant differences between locations for salinity (Table 3). Post-hoc SNK procedures revealed three distinct groupings: Safety Harbor was grouped on its own with the lowest salinity; in contrast, Fort De Soto and Sunshine Skyway clustered together with the highest salinity. The rest of the locations formed a group representing intermediate salinity (Table 3).

There was a strong negative relationship between mussel abundance and salinity (Figure 5). The greatest densities were found at the location with lowest salinity (Safety Harbor) and the lowest densities were found at the locations with the highest salinities (Fort De Soto and Sunshine Skyway) (Figure 5).

Population structure showed greater heterogeneity (i.e., characterised by mussels of different sizes), at locations of intermediate salinity compared to sites of highest/lowest salinity (Figure 6). Moreover, at locations characterised by extreme salinities (i.e. Safety Harbor, Sunshine Skyway and Fort De Soto), no individuals in the larger size class were found during the first survey in December 2007.

4. Discussion

We provide strong evidence supporting the hypothesis that thermal stress related to exposure to cold air temperatures during emersion was the primary factor underpinning the mortality event for mussels occupying intertidal substrata across sites in Tampa Bay in 2008. Our observations indicate that mussels recruit back to the intertidal in early summer. Importantly, in the two years subsequent to our initial bay-wide survey, we found that the winter die-off was repeated at three sites where mussels were abundant in the 2007 survey and extreme cold air temperatures were reported during the winters of 2008/2009 and 2009/2010. These events do not appear to be unique as a similar mortality event occurred in the mussel populations on the northeast coast of Florida in 2007/2008 (M. Gilg, pers. comm.). *Perna viridis* is also known to experience winter die-offs in Japan (Umemori and Horikoshi, 1991; Kazuhiro and Sekiguchi, 2000; Zvyagintsev, 2003) where it is also considered an invasive species.

During 2007/2008 an extreme weather event occurred in Tampa Bay when air temperatures dropped to near freezing for a period of 6 hours during low water. Subsequent to this cold snap, water temperatures dipped slightly but it is unlikely that this slight drop in water temperature led to the bay-wide mortality event observed in *P. viridis*. A similar pattern was true for air and water temperatures from 2008-2010. It is extremely likely that the prolonged exposure to low air temperatures caused the mortality events for *P. viridis* across Tampa Bay. Although not tested experimentally during the present study, previous investigations have found that cold water temperature causes mortality of *P. viridis* (Sivalingam, 1977; Urian et al., 2010). Little work has been carried out on the effects of cold air temperatures on *P. viridis*, but a recent laboratory study found that the mortality was significantly higher in mussels exposed to cold air temperatures ≤14°C and that smaller individuals were less tolerant of changes in air temperature than larger ones (Urian et al., 2010).

Thermal stress is widely cited as the dominant physical stress in intertidal habitats (Garrity, 1984; Helmuth and Hofmann, 2001) and is reported to cause mortality events on both temperate (Orton, 1933; Lewis, 1954; Harley et al., 2006) and tropical shores (Williams and Morritt, 1995; Chan et al., 2006; Firth and Williams, 2009). Many studies focus on the effects of warm thermal stress on the physiological and behavioural responses of organisms (Somero, 2002; Jones et al., 2009; Denny et al., 2011; Sorte et al., 2011) while the effects of cold thermal stress are often neglected, particularly at lower latitudes (but see Urian et al., 2010). Furthermore, despite many intertidal organisms being exposed to aerial conditions during low water, less attention has been directed at assessing the effects of extreme air temperatures in comparison to extreme water temperatures. This focus is perhaps surprising as larger fluctuations in temperature are more likely to occur in aerial environments than aquatic environments due to the buffering capacity of water (Marshall and Plumb, 2008). In a subtropical setting such as described here, low aerial temperatures may be an important mechanism by which mussels are prevented from excluding other fouling organisms, such as oysters and barnacles.

Two of the predictions accompanying discussions of global climate change are (1) a rise in the mean sea surface temperature globally and (2) an increase in the occurrence, intensity and magnitude of extreme weather events (IPCC, 2007). Stachowicz et al., (2002) proposed that changing maximum and minimum temperatures rather than shifts in annual means could account for the greatest impacts of climate change on marine communities. Our findings on the green mussel provide support for this proposal. Future studies on changes in community assemblages that follow assemblages across years both with and without extreme weather events are necessary.

It is well documented that climate warming on the scale of decades can alter the composition of marine communities by facilitating the poleward spread of warm-adapted species (Southward et al., 1995; Sagarin et al., 1999; Stachowicz et al., 2002; Mieszkowska et al., 2005). Climate is typically defined as the mean of weather over a large temporal scale (>30 years) (Helmuth et al., 2006). Specifically, Stenseth et al., (2003) defined weather as the fluctuation in short-term localised atmospheric conditions which encompass air temperature, solar radiation, cloud cover, precipitation, and wind. Recently, there has been a surge of interest on the effects of multiple environmental stressors (Atalah and Crowe, 2010; Crain, 2008; Firth and Williams, 2009; Fitch and Crowe, 2011) and extreme weather events (Harley et al., 2006; Hughes et al., 2009; Sorte et al., 2010a,b; Wethey et al., 2011) on marine communities and increasingly, results from field studies appear to justify such an emphasis.

For example in the United Kingdom, the extremely cold winter of 1962/1963 lasted from late December 1962 through to early March 1963. During this time the mean air temperatures ranged between -3.2°C and 0.2°C (Crisp, 1964). As a result of the prolonged cold temperatures, a contraction of the northern range edge of many southern warm-adapted species was recorded, particularly around North Wales (Crisp, 1964). With the continuing trend in climate warming, some of these species (e.g. *Sabellaria alveolata*, *Osilinus lineatus*) are now beginning to recolonise locations where they previously occurred (Mieszkowska et al., 2005, 2007; Hawkins pers. comm.). These recolonisations have implications for community structure and functioning particularly when the species involved are keystone species or provide habitat for other species (e.g. mussels, oysters: see Hawkins et al., 2009).

The results of the present study suggest that physiological stress driven by extreme weather may be responsible for limiting the invasion success of the green mussel in a subtropical area. The blue mussel, *Mytilus galloprovincialis* is an invasive species on the California coast. Lockwood and Somero (2011) discuss how physical factors, such as temperature, could be limiting its northward spread in California, while simultaneously facilitating its competitive ability.

The unusually cold weather experienced in south Florida in January 2010 also resulted in the mortality of the invasive Burmese Python (*Python molurus bivattus*) in Everglades National Park (Mazzotti et al., 2010). Similarly, the cold winter in 2009-2010 had a significant impact on intertidal marine fauna in northern Europe. Wethey et al., (2011) found that southern warm-adapted (native) barnacle species (*Chthamalus*) suffered recruitment failure, but no adult mortality in France.

In the short term, weather may be responsible for the temporary retreat of a population's distribution at the edge of its geographic range (Crisp, 1964; Baker et al., 2007; Urian et al., 2010). In the longer-term, it is expected that climate warming will facilitate both the poleward movement of native species (Mieszkowska et al., 2005; Hiddink and ter Hofstede, 2008) and the spread of non-indigenous species to new locations (Stachowicz et al., 2002; Sorte et al., 2010a; Sorte et al., 2010b). This interaction between global climate change and human-induced biological invasions may ultimately lead to biotic homogenisation - the process of gradual replacement of native communities by locally expanding non-native species (Olden et al., 2004). The challenge now is to forecast when and where these changes are likely to occur and devise adaptive management strategies in order to mitigate any potential negative impacts to native biodiversity.

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TABLES

Table 1. Summary of minimum air and corresponding water temperatures (^oC) from PORTS for St Petersburg, Florida on dates for which lowest temperatures of the month are recorded or for those dates when air temperature was <15^oC. Duration (hours) when air temperature subsequent to date reported was continuously less than 15^oC is also noted.

Date	Low air temperature (^oC)	Low water temperature (^oC)	Duration (hours)
17/12/2007	6	21	18
04/01/2008	1	18	64
15/02/2008	7	21	6
28/11/2008	7	20	6
20/01/2009	4	18	36
04/02/2009	3	17	18
05/12/2009	9	21	6
09/12/2009	9	20	24
28/12/2009	9	19	12
10/01/2010	0	12	120
14/02/2010	8	17	6

Table 2. Analysis of variance (ANOVA) to assess differences in *P. viridis* density at 9 locations in Tampa Bay in December 2007, February 2008 and May 2008, (*** = P<0.001).

Source	**df**	**MS**	***F***
Survey	2	5450.73	13.34***
Location	8	387.78	0.95
Survey × Location	16	408.51	8.29***
RES	297	49.28	

Table 3. Analyses of variance (ANOVA) to test the differences in sea surface temperature (°C) and salinity (ppt) between locations. (**=P<0.01; *** = P<0.001).

		Salinity	
Source	**df**	**MS**	**F**
Location	8	79.43	27.72***
Total	99		
Cochrans *C*		P<0.05	
Transformation		None	
SNK tests	SH< MB=BP=GB=DI=FI=PI=SS<<FS		

FIGURE LEGENDS

Figure 1. Map of survey locations in Tampa Bay. SH = Safety Harbor; MB = McKay Bay; BP = Ballast Point; GB = Gandy Bridge; DI = Davis Islands; FI = Fantasy Island; PI = Picnic Island; SS = Sunshine Skyway; FS = Fort De Soto.

Figure 2. Mean abundance of *Perna viridis* in quadrats ($0.04m^2$) at each location: Safety Harbor; McKay Bay; Ballast Point; Gandy Bridge; Davis Islands; Fantasy Island; Picnic Island; Sunshine Skyway; Fort De Soto

Figure 3. Mean daily air and water temperature (ºC) measured at St. Petersburg, Florida during the period of the study (11/12/2007 to 19/02/2008). Data obtained from http://tidesandcurrents.noaa.gov

Figure 4. Hourly air and water temperatures (ºC) and water height (m) relative to MLW measured at St. Petersburg, Florida during the period of cold weather between 2nd and 4th February 2008. Arrow indicates low water (4.13 m below MTL) coinciding with extremely cold air temperature (0.5ºC). Data obtained from http://tidesandcurrents.noaa.gov

Figure 5. The relationship between mean abundance of *P. viridis* per quadrat and salinity (ppt). Only data from December 2007 survey is used here. ($F = 44.46$, $P<0.001$).

Figure 6. Size-frequency distributions of *P. viridis* across locations in Tampa Bay. Locations are grouped in order of increasing salinity from left to right. SH = Safety Harbor; MB=McKay Bay; BP = Ballast Point; Gandy Bridge; DI = Davis Islands; FI = Fantasy Island; PI = Picnic Island; SS = Sunshine Skyway; FS = Fort De Soto.

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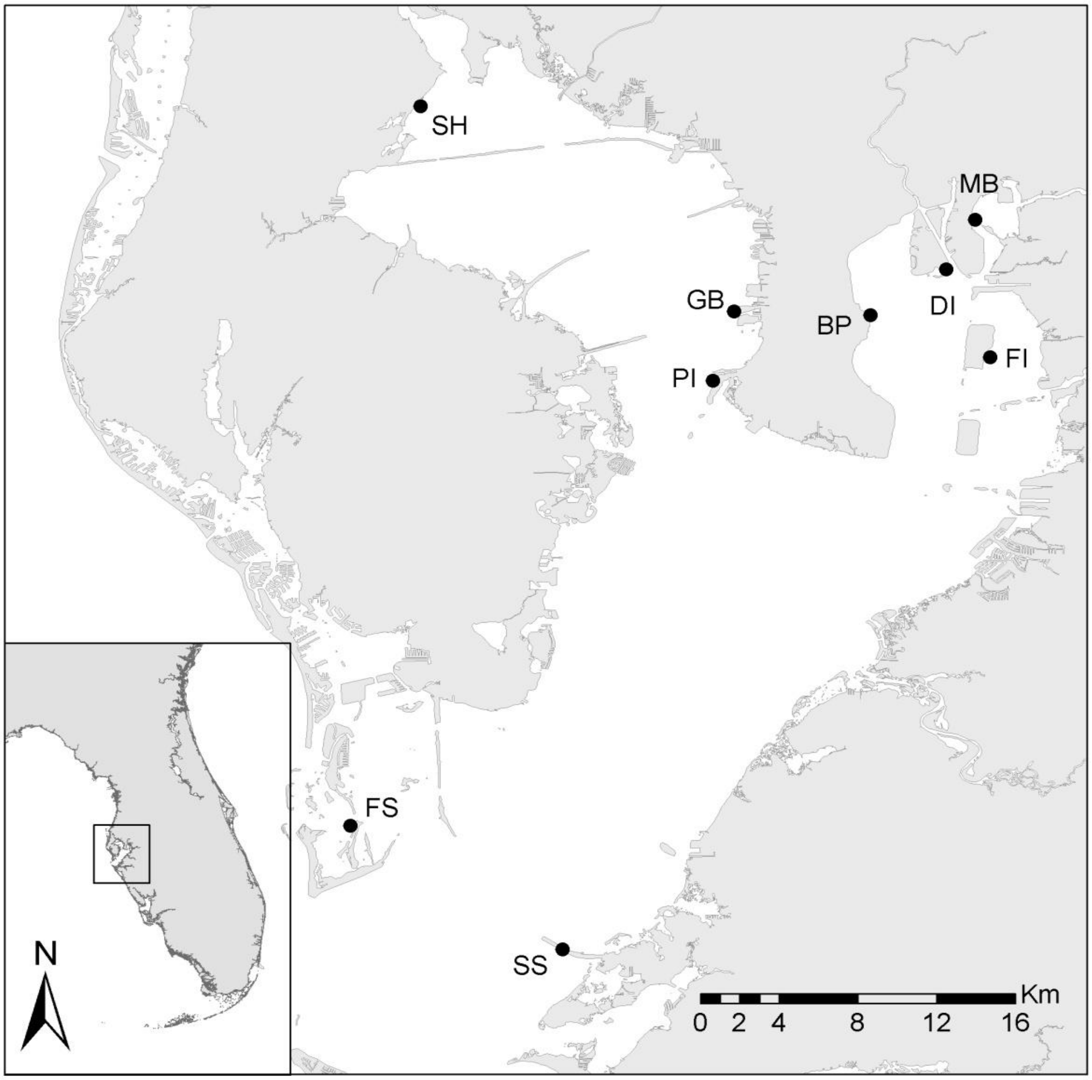

633

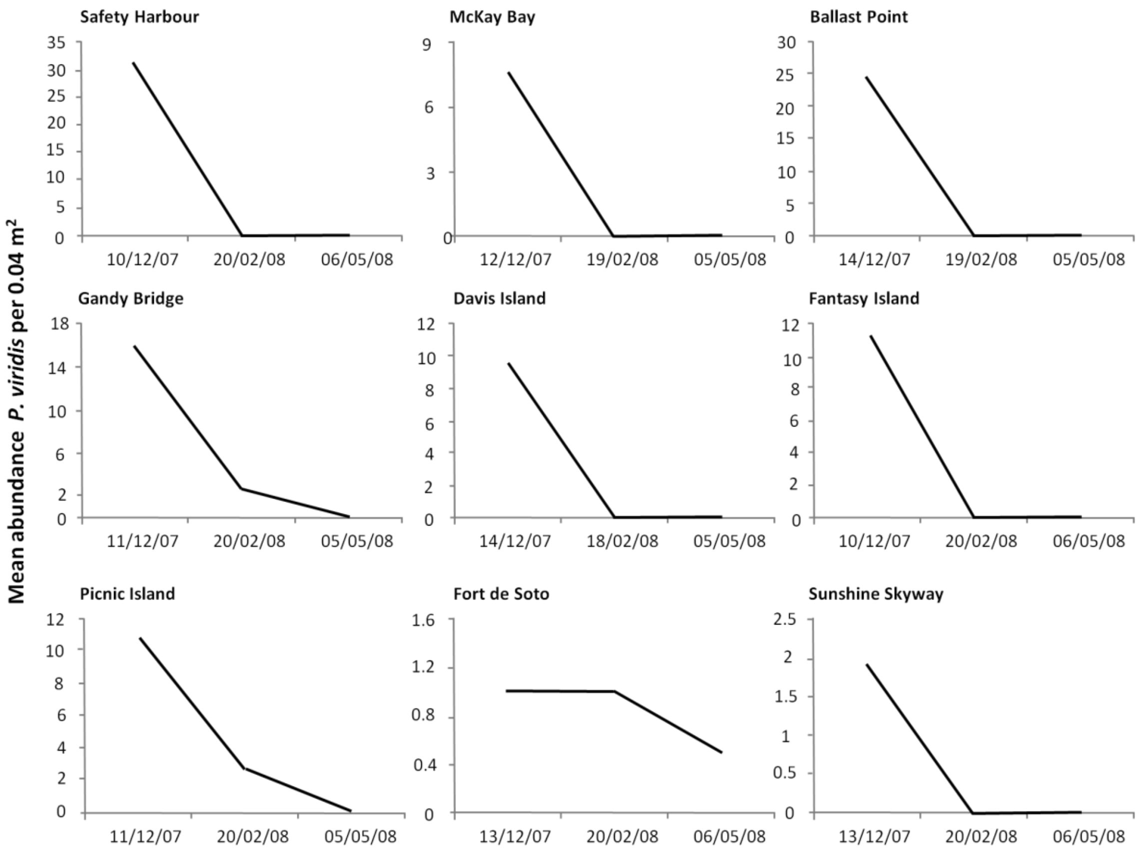
Mean abundance *P. viridis* per 0.04 m²
Safety Harbour
10/12/07
20/02/08
06/05/08
McKay Bay
12/12/07
19/02/08
05/05/08
Ballast Point
14/12/07
19/02/08
05/05/08
Gandy Bridge
11/12/07
20/02/08
05/05/08
Davis Island
14/12/07
18/02/08
05/05/08
Fantasy Island
10/12/07
20/02/08
06/05/08
Picnic Island
11/12/07
20/02/08
05/05/08
Fort de Soto
13/12/07
20/02/08
06/05/08
Sunshine Skyway
13/12/07
20/02/08
06/05/08

Figure 2.

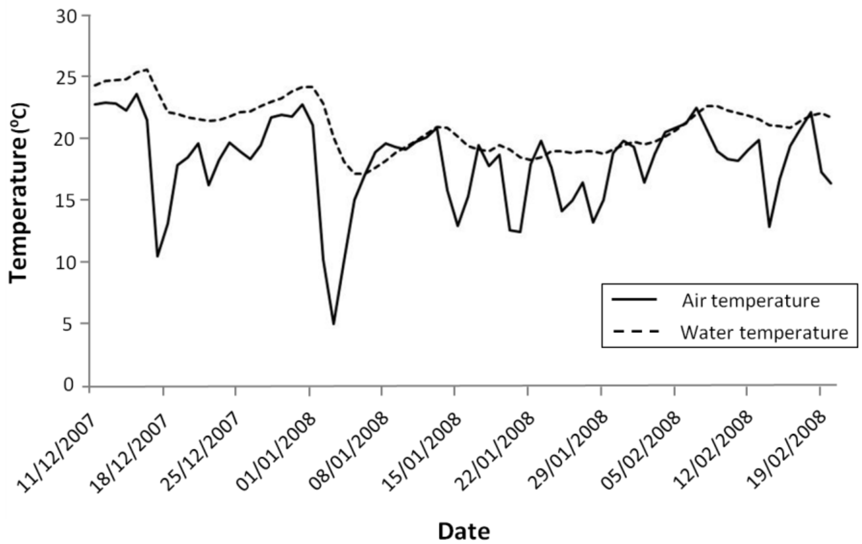
Temperature (ºC)
30
25
20
15
10
5
0
Air temperature
Water temperature
11/12/2007
18/12/2007
25/12/2007
01/01/2008
08/01/2008
15/01/2008
22/01/2008
29/01/2008
05/02/2008
12/02/2008
19/02/2008
Date

Figure 3.

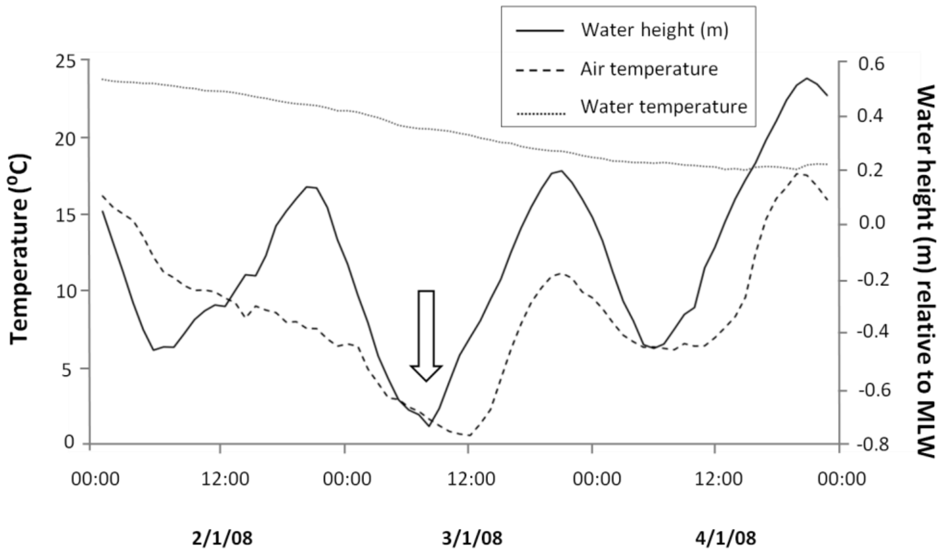
Water height (m)
Air temperature
Water temperature
Temperature (°C)
Water height (m) relative to MLW
25
20
15
10
5
0
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
00:00
12:00
00:00
12:00
00:00
12:00
00:00
2/1/08
3/1/08
4/1/08

Figure 4.

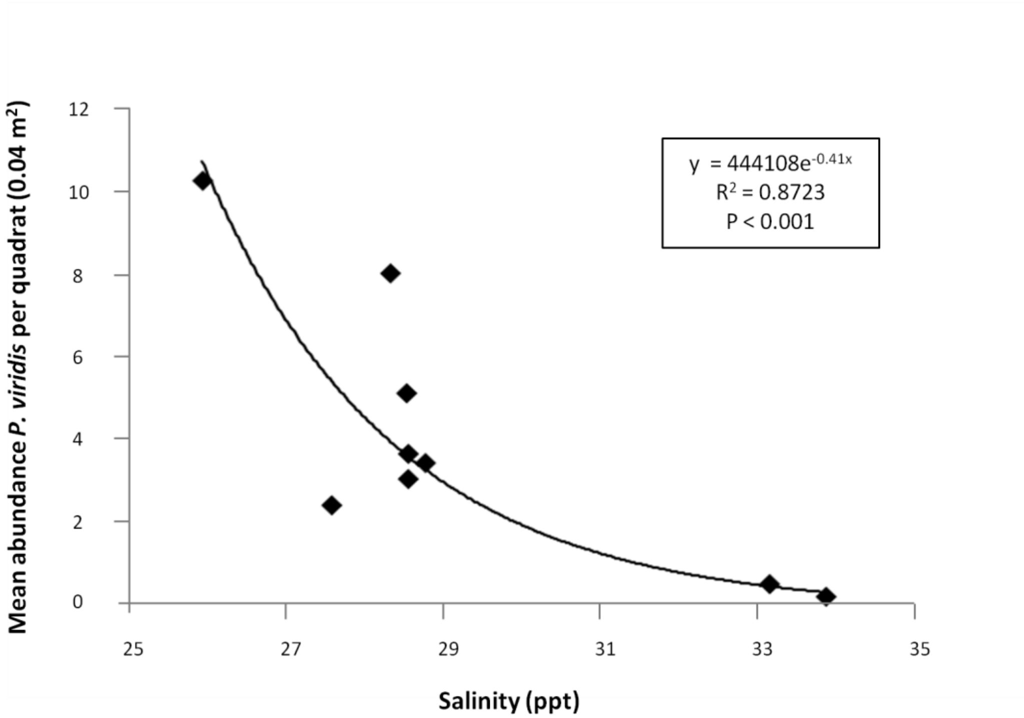
y = 444108e^-0.41x
R² = 0.8723
P < 0.001
Mean abundance P. viridis per quadrat (0.04 m²)
Salinity (ppt)
0
2
4
6
8
10
12
25
27
29
31
33
35

Figure 5.

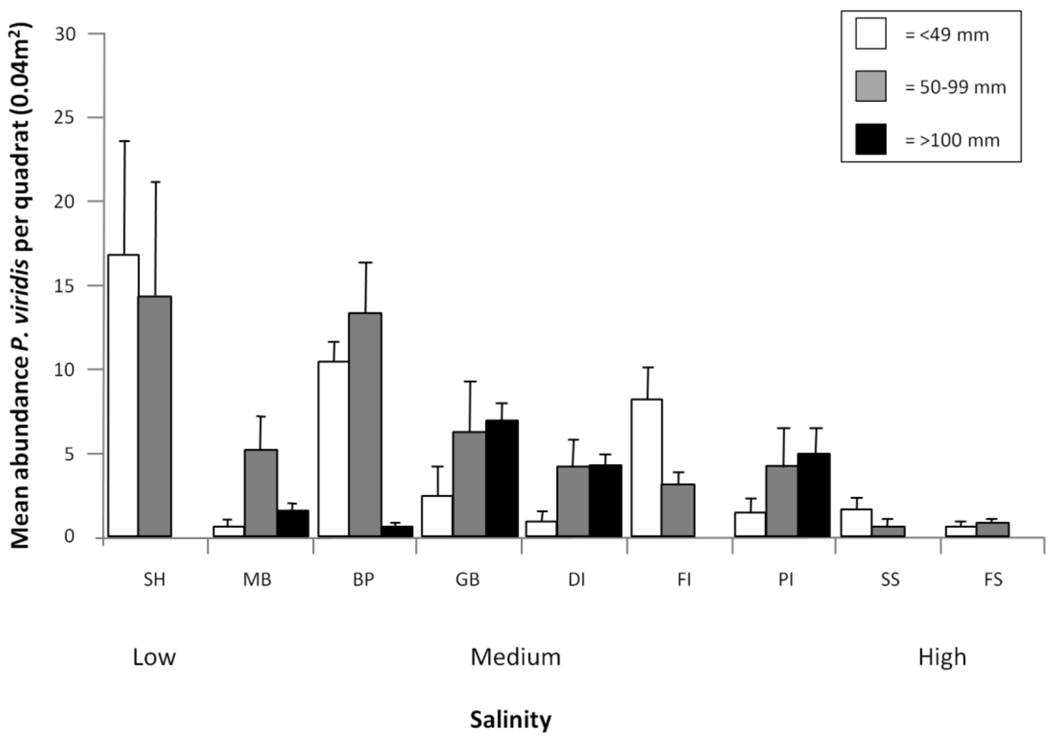
Mean abundance P. viridis per quadrat (0.04m²)
30
25
20
15
10
5
0
= <49 mm
= 50-99 mm
= >100 mm
SH
MB
BP
GB
DI
FI
PI
SS
FS
Low
Medium
High
Salinity

Figure 6.