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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

Firth, LB

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5	
6	AUTHORS:
7	Louise B. Firth ^{a,b}
8	Antony M. Knights ^{c,d}
9	Susan S. Bell ^a
10	
11	^a Department of Integrative Biology, University of South Florida, 4202 East Fowler
12	Avenue, Tampa, FL 33620-5550, USA
13	^b Current address: School of Ocean Sciences, Bangor University, Menai Bridge,
14	Anglesey, LL59 5AB, United Kingdom
15	^c Department of Marine Science, Coastal Carolina University, Conway, SC 29528, USA
16	^d Current address: School of the Environment, University of Liverpool, Biosciences
17	Building, Crown Street, Liverpool, L69 7ZB, United Kingdom
18	
19	* Corresponding author: <u>l.firth@bangor.ac.uk</u> , tel (+44) 01248 388859
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32 Abstract

33 Global climate change and invasive species represent two of the biggest threats to the 34 environment. Biological communities are responding to global climate change through 35 poleward shifts in distribution, and changes in abundance and phenology of both native 36 and non-native species. An increase in the frequency and magnitude of extreme weather 37 events is predicted with global climate change. Much is known about mortality events of 38 marine organisms in relation to warm thermal stress with relatively little known about 39 cold thermal stress, particularly in the tropics. Intertidal species are particularly 40 susceptible to fluctuations in aerial conditions and many are considered indicators of 41 climate change. *Perna viridis* is a recent invader to the United States where it fouls hard 42 substrates and soft sediment habitats. During winter 2007-2008, a mortality event was 43 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 44 hours during low water. The minimum air temperature recorded was 0.53°C. During this 45 46 period water temperature remained relatively constant ($\sim 20^{\circ}$ C). We provide strong 47 evidence supporting the hypothesis that thermal stress relating to exposure to cold air 48 temperatures during emersion was the primary factor underpinning the mortality event. 49 Similar mortality events occurred in 2009 and 2010, also coinciding with prolonged 50 exposure to low air temperatures.

51

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.

58

59 1. Introduction

60 Global climate change and invasive non-native species represent two of the most serious 61 global threats to biodiversity and the environment (Stachowicz et al., 2002; Ward and 62 Masters 2007). Biological communities are responding to global climate change through 63 poleward shifts in distribution, and changes in abundance and phenology (Sims et al., 64 2004; Mieszkowska et al., 2005; Hiddink and ter Hofstede, 2008; Moore et al., 2010; 65 Aprahamian et al., 2010; Wethey et al., 2011). Changes in distribution and associated 66 species interactions have the potential to greatly affect the structure and functioning of 67 communities (Moore et al., 2007; Firth et al., 2009). Climate change not only facilitates a 68 shift in the distribution of indigenous species but also the establishment and extension in 69 range of non-indigenous species (Stachowicz et al., 2002; Sorte et al., 2010a, b). 70 71 Furthermore, global climate change is expected to lead to an increase in the frequency 72 and magnitude of extreme weather events (IPCC, 2007). Fluctuation in temperature is 73 well documented as a driver of mortality in many marine species at temperate and 74 subpolar latitudes (Orton, 1933; Harley et al., 2006; Coma et al., 2009; Firth and 75 Williams, 2009; Sorte et al., 2011) and disease outbreak is often associated with 76 increased temperatures (Harvell et al., 1999; Bruno et al., 2007). Conversely, mortality 77 events driven by cold thermal stress have received less attention, particularly at 78 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).

80

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).

86

87 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).

89 Organisms living in the intertidal zone are of marine origin but experience terrestrial

90 conditions daily during low tide. The upper distributional limits of intertidal organisms 91 are set by physical factors such as thermal and desiccation stress (Connell, 1972; Somero, 92 2002; Harley et al., 2006; Hawkins et al., 2008, 2009). This vulnerability to terrestrial 93 conditions infers that variations in climatic conditions are likely to elicit strong responses 94 in intertidal organisms and result in changes in distribution and community structure and 95 functioning (Fields et al., 1993; Lubchenco et al., 1993; Helmuth et al., 2006). The 96 responses of intertidal organisms to environmental conditions has allowed for them to 97 serve as proxies for changes occurring offshore (Mieszkowska et al., 2005).

98

99 The Asian green mussel, *Perna viridis*, is native to the tropical Indo-Pacific region, 100 primarily distributed along the Indian and southeast Asian coasts (Siddall, 1980; Vakily, 101 1989; Rajagopal et al., 2006). This species was first recorded in North America in 1999, 102 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 103 104 water exchange (Power et al., 2004). The mussel has since spread to both the Gulf and 105 Atlantic coasts of Florida (Ingrao et al., 2001; Baker et al., 2007) occurring as far 106 eastwards as Panama City on the Florida Panhandle and north towards Georgia (Power et 107 al., 2004). A recent survey indicated that individuals have extended as far north as South 108 Carolina (Benson, 2010). The mussel is found attached to the many forms of hard 109 structure introduced by man (pilings, docks, bridge supports) as the natural coastline is 110 characterized by soft sediments. It occurs on these hard substrates both in the intertidal 111 and in the subtidal zones, where it is also known to occur on soft sediments and among 112 sea grass beds (Bell, pers. obs). Little is known about the impact of this species on native 113 biodiversity but as its range expands, new interactions with indigenous species are likely 114 to occur. For example, one observation suggests that *P. viridis* may out-compete the 115 commercially important native eastern oyster, Crassostrea virginica. During a survey of 116 P. viridis in Tampa Bay, Baker et al., (2007) observed a layer of dead C. virginica shells 117 covered by *P. viridis*. Where living *C. virginica* was found, individuals were limited to 118 the upper few centimetres of the intertidal, above P. viridis. Subsequent to a P. viridis 119 winter die-off in January 2003, Baker et al., (2007) were unable to find any living C. 120 virginica in the area previously occupied by *P. viridis*. It is well documented that

- 121 mussels provide refuge and habitat for a wide variety of associated organisms (Seed,
- 122 1996) and that this function can vary with size of mussels (O'Connor and Crowe, 2007).
- 123 Little is known about the biodiversity associated with *P. viridis* patches, but due to
- 124 differences in size of individuals and patch complexity between oysters and mussels, it is
- 125 likely that expansion of the green mussel will have potentially long-term effects on
- 126 diversity of epibiota and mobile fauna.
- 127

While ecological information on the green mussel is quite limited after its spread toTampa Bay, field observations at a small number of locations suggested that cold winter

130 temperatures might be responsible for an observed temporary disappearance of *P. viridis*

131 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

134 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 eventsoccur in Tampa Bay.

- 137
- 138

139 2. Materials & methods

140 2.1 Study sites

141 Tampa Bay, Florida exhibits an increasing salinity gradient from north to south (Barber et142 al., 2005). Nine survey locations were selected across a wide area of Tampa Bay, for

143 which salinity data were available for the 12 months prior to December 2007, and

144 comprised hard substrata (bridge pilings, pier pilings or pontoons) for attachment of

145 mussels. Locations (Figure 1) that were surveyed were Safety Harbor Pier; McKay Bay

146 Bridge; Ballast Point Pier; Gandy Bridge; Davis Islands Slipway; Fantasy Island Pier;

147 Picnic Island Pier; Sunshine Skyway Bridge and Fort De Soto Slipway.

148

149 At each location, 12 quadrats (20×20 cm) were placed 1 m below the mean high water

150 mark on all orientations of pilings or just below the water mark on pontoons. All mussels

151 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 152 153 December 2007 in order to establish baseline information on the distribution and 154 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 155 156 dead. Following this, a complete resurvey of all locations was carried out from 18-20th 157 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 158 159 categorised into size classes based on their antero-postero length: small (<49 mm); 160 medium (50-99 mm); and large (>50 mm). In addition, the presence/absence of mussels 161 was noted in the intertidal zone in summer and winter months at three sites: Courtney 162 Campbell Causeway (near Safety Harbor), Gandy Bridge and Sunshine Skyway Bridge 163 from 2008-2010. 164 165 166 2.2 Physico-chemical parameters 167 The Environmental Protection Commission of Hillsborough County collected monthly 168 salinity (ppt) measurements by placing a probe just below the surface of the water at all 169 sampling locations across Tampa Bay between January-December 2007. Additionally, 170 data on air and water temperature on a 6 hour basis was obtained from a meteorological 171 station near St. Petersburg Florida and supplied by TB-PORTS (Tampa Bay Physical 172 Oceanographic Real-Time System) for all dates from 2007-2010 (Table 1). 173 174 2.3 Analyses 175 Analysis of variance (ANOVA) was used to test the *a posteriori* hypothesis that a 176 mortality event occurred in Tampa Bay using density of mussels as the dependent 177 variable. Two-factor ANOVA was performed using the factors: survey (3 levels, random, 178 orthogonal); and location (9 levels, random, orthogonal) with 12 replicates. GMAV® 179 version 5 for Windows was used for computations (Underwood and Chapman, 1998).

180 Cochran's test was used to test for heterogeneity of variances and Student-Newman-

181 Keuls (SNK) procedure was used to make *post hoc* comparisons among levels of

182 significant terms. Variances were heterogeneous, but it was not possible to transform the183 data.

184

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).

189

190 **3. Results**

191 *3.1 Mussel survey*

192 324 quadrats were sampled comprising a total of 1452 mussels. Total mussel abundance

193 (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)

195 December 2007) was also highest at Safety Harbor (31.3), then Ballast Point (24.6) and

196 lowest at Sunshine Skyway (1.91) and Fort De Soto (1.0) with other locations

197 characterised by populations of intermediate density (Figure 2).

198

199 A bay-wide mortality event of *Perna viridis* occurred between December 2007 and May 200 2008 (Figure 2). On the second sampling period in February 2008, live mussels were only 201 recorded at Gandy Bridge, Picnic Island and Fort De Soto (Table 2, Figure 2). At 202 locations where no live mussels were observed within the quadrats, a broad visual search 203 was done of the sampling site for any live mussels but none were recorded. Dead mussel 204 shells were observed attached to the substrate or on the sea-bottom at many of the 205 locations, indicating recent mortality. On the third sampling period (May 2008), 206 populations at both Gandy Bridge and Picnic Island had also decreased to zero with Fort 207 De Soto being the only location where any live mussels were recorded (Figure 2). 208 209 Surveys in 2009-2010 also indicated the disappearance of mussels after unusually cold 210 temperatures. While mussels were present in October 2008 and 2009, none were found 211 in January 2009 or 2010 on structures in the intertidal zone at the study sites.

212

213 *3.2 Temperature data*

214 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
- 216 19/02/2008 (Figure 3). Water temperature was relatively constant, remaining above 20°C
- 217 (20-25) for the majority of the period. Water temperature twice dipped slightly below
- 218 20°C (17-19) between 4-11th January and again between 16th January and 3rd February.
- 219
- 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
- 222 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
- 224 (<2°C) for 6 hours when a minimum temperature of 0.53°C was recorded at 12:00 during
- low water (Figure 4).
- 226

227 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

- 229 0°C once and remained lower than 15°C for at least 3 days (Table 1).
- 230

231 *3.3 Mussel abundance in relation to salinity*

232 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-

235 December 2007.

236

237 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

241 intermediate salinity (Table 3).

242

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).

247

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.

- 253
- 254

255 **4. Discussion**

256 We provide strong evidence supporting the hypothesis that thermal stress related to 257 exposure to cold air temperatures during emersion was the primary factor underpinning 258 the mortality event for mussels occupying intertidal substrata across sites in Tampa Bay 259 in 2008. Our observations indicate that mussels recruit back to the intertidal in early 260 summer. Importantly, in the two years subsequent to our initial bay-wide survey, we 261 found that the winter die-off was repeated at three sites where mussels were abundant in 262 the 2007 survey and extreme cold air temperatures were reported during the winters of 263 2008/2009 and 2009/2010. These events do not appear to be unique as a similar mortality 264 event occurred in the mussel populations on the northeast coast of Florida in 2007/2008 265 (M. Gilg, pers. comm.). Perna viridis is also known to experience winter die-offs in 266 Japan (Umemori and Horikoshi, 1991; Kazuhiro and Sekiguchi, 2000; Zvyagintsev, 267 2003) where it is also considered an invasive species. 268

269 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.

271 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*.

273 *viridis*. A similar pattern was true for air and water temperatures from 2008-2010. It is

274 extremely likely that the prolonged exposure to low air temperatures caused the mortality 275 events for *P. viridis* across Tampa Bay. Although not tested experimentally during the 276 present study, previous investigations have found that cold water temperature causes 277 mortality of *P. viridis* (Sivalingam, 1977; Urian et al., 2010). Little work has been carried 278 out on the effects of cold air temperatures on P. viridis, but a recent laboratory study 279 found that the mortality was significantly higher in mussels exposed to cold air 280 temperatures $\leq 14^{\circ}$ C and that smaller individuals were less tolerant of changes in air 281 temperature than larger ones (Urian et al., 2010).

282

283 Thermal stress is widely cited as the dominant physical stress in intertidal habitats 284 (Garrity, 1984; Helmuth and Hofmann, 2001) and is reported to cause mortality events on 285 both temperate (Orton, 1933; Lewis, 1954; Harley et al., 2006) and tropical shores 286 (Williams and Morritt, 1995; Chan et al., 2006; Firth and Williams, 2009). Many studies 287 focus on the effects of warm thermal stress on the physiological and behavioural 288 responses of organisms (Somero, 2002; Jones et al., 2009; Denny et al., 2011; Sorte et al., 289 2011) while the effects of cold thermal stress are often neglected, particularly at lower 290 latitudes (but see Urian et al., 2010). Furthermore, despite many intertidal organisms 291 being exposed to aerial conditions during low water, less attention has been directed at 292 assessing the effects of extreme air temperatures in comparison to extreme water 293 temperatures. This focus is perhaps surprising as larger fluctuations in temperature are 294 more likely to occur in aerial environments than aquatic environments due to the 295 buffering capacity of water (Marshall and Plumb, 2008). In a subtropical setting such as 296 described here, low aerial temperatures may be an important mechanism by which 297 mussels are prevented from excluding other fouling organisms, such as oysters and 298 barnacles.

299

300 Two of the predictions accompanying discussions of global climate change are (1) a rise

301 in the mean sea surface temperature globally and (2) an increase in the occurrence,

302 intensity and magnitude of extreme weather events (IPCC, 2007). Stachowicz et al.,

303 (2002) proposed that changing maximum and minimum temperatures rather than shifts in

304 annual means could account for the greatest impacts of climate change on marine

305 communities. Our findings on the green mussel provide support for this proposal. Future
306 studies on changes in community assemblages that follow assemblages across years both
307 with and without extreme weather events are necessary.

308

309 It is well documented that climate warming on the scale of decades can alter the 310 composition of marine communities by facilitating the poleward spread of warm-adapted 311 species (Southward et al., 1995; Sagarin et al., 1999; Stachowicz et al., 2002; 312 Mieszkowska et al., 2005). Climate is typically defined as the mean of weather over a 313 large temporal scale (>30 years) (Helmuth et al., 2006). Specifically, Stenseth et al., 314 (2003) defined weather as the fluctuation in short-term localised atmospheric conditions 315 which encompass air temperature, solar radiation, cloud cover, precipitation, and wind. 316 Recently, there has been a surge of interest on the effects of multiple environmental 317 stressors (Atalah and Crowe, 2010; Crain, 2008; Firth and Williams, 2009; Fitch and 318 Crowe, 2011) and extreme weather events (Harley et al., 2006; Hughes et al., 2009; Sorte 319 et al., 2010a,b; Wethey et al., 2011) on marine communities and increasingly, results 320 from field studies appear to justify such an emphasis.

321

322 For example in the United Kingdom, the extremely cold winter of 1962/1963 lasted from 323 late December 1962 through to early March 1963. During this time the mean air 324 temperatures ranged between -3.2°C and 0.2°C (Crisp, 1964). As a result of the 325 prolonged cold temperatures, a contraction of the northern range edge of many southern 326 warm-adapted species was recorded, particularly around North Wales (Crisp, 1964). With 327 the continuing trend in climate warming, some of these species (e.g. Sabellaria alveolata, 328 *Osilinus lineatus*) are now beginning to recolonise locations where they previously 329 occurred (Mieszkowska et al., 2005, 2007; Hawkins pers. comm.). These recolonisations 330 have implications for community structure and functioning particularly when the species 331 involved are keystone species or provide habitat for other species (e.g. mussels, oysters: 332 see Hawkins et al., 2009).

333

The results of the present study suggest that physiological stress driven by extremeweather may be responsible for limiting the invasion success of the green mussel in a

336 subtropical area. The blue mussel, *Mytilus galloprovincialis* is an invasive species on the

337 California coast. Lockwood and Somero (2011) discuss how physical factors, such as

temperature, could be limiting its northward spread in California, while simultaneouslyfacilitating its competitive ability.

340

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)

345 found that southern warm-adapted (native) barnacle species (*Chthamalus*) suffered

346 recruitment failure, but no adult mortality in France.

347

348 In the short term, weather may be responsible for the temporary retreat of a population's 349 distribution at the edge of its geographic range (Crisp, 1964; Baker et al., 2007; Urian et 350 al., 2010). In the longer-term, it is expected that climate warming will facilitate both the 351 poleward movement of native species (Mieszkowska et al., 2005; Hiddink and ter 352 Hofstede, 2008) and the spread of non-indigenous species to new locations (Stachowicz 353 et al., 2002; Sorte et al., 2010a; Sorte et al., 2010b). This interaction between global 354 climate change and human-induced biological invasions may ultimately lead to biotic 355 homogenisation - the process of gradual replacement of native communities by locally 356 expanding non-native species (Olden et al., 2004). The challenge now is to forecast when 357 and where these changes are likely to occur and devise adaptive management strategies in 358 order to mitigate any potential negative impacts to native biodiversity.

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- 360

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366

368 TABLES

- 369 Table 1. Summary of minimum air and corresponding water temperatures (°C) from
- 370 PORTS for St Petersburg, Florida on dates for which lowest temperatures of the month
- are recorded or for those dates when air temperature was $<15^{\circ}$ C. Duration (hours) when
- air temperature subsequent to date reported was continuously less than 15°C is also noted.
- 373

Date	Low air temperature	Low water temperature	Duration
	(C)	(C)	(nours)
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

374

375

376

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

379 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	

380

- 381
- 382

383

- 385 Table 3. Analyses of variance (ANOVA) to test the differences in sea surface temperature
- 386 (°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< M	IB=BP=GB=D	I=FI=PI=SS< <fs< td=""></fs<>

FIGURE LEGENDS

- 392
- 393 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
- 395 = Picnic Island; SS = Sunshine Skyway; FS = Fort De Soto.
- 396
- Figure 2. Mean abundance of *Perna viridis* in quadrats (0.04m²) at each location: Safety
- Harbor; McKay Bay; Ballast Point; Gandy Bridge; Davis Islands; Fantasy Island; Picnic
 Island; Sunshine Skyway; Fort De Soto
- 400
- 401 Figure 3. Mean daily air and water temperature (°C) measured at St. Petersburg, Florida
- 402 during the period of the study (11/12/2007 to 19/02/2008). Data obtained from
- 403 <u>http://tidesandcurrents.noaa.gov</u>
- 404
- 405 Figure 4. Hourly air and water temperatures (°C) and water height (m) relative to MLW
- 406 measured at St. Petersburg, Florida during the period of cold weather between 2nd and 4th
- 407 February 2008. Arrow indicates low water (4.13 m below MTL) coinciding with
- 408 extremely cold air temperature $(0.5^{\circ}C)$. Data obtained from
- 409 <u>http://tidesandcurrents.noaa.gov</u>
- 410
- 411 Figure 5. The relationship between mean abundance of *P. viridis* per quadrat and salinity
- 412 (ppt). Only data from December 2007 survey is used here. (F = 44.46, P<0.001).
- 413
- 414 Figure 6. Size-frequency distributions of *P. viridis* across locations in Tampa Bay.
- 415 Locations are grouped in order of increasing salinity from left to right. SH = Safety
- 416 Harbor; MB=McKay Bay; BP = Ballast Point; Gandy Bridge; DI = Davis Islands; FI =
- 417 Fantasy Island; PI = Picnic Island; SS = Sunshine Skyway; FS = Fort De Soto.
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713 Figure 6.