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RHODES AND TURNER: PHYSIOLOGY OF HERMIT CRABS

SALINITY TOLERANCE AND OSMOTIC RESPONSE OF THE
ESTUARINE HERMIT CRAB *PAGURUS MACLAUGHLINAE*
IN THE INDIAN RIVER LAGOON, FLORIDA

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20 ABSTRACT

21 *Pagurus maclaughlinae* is the most common hermit in the Indian River Lagoon System. Wide
22 variations in lagoonal salinity make it likely that *P. maclaughlinae* is euryhaline and that other
23 hermit species in the area are more stenohaline, at least in some stages of their life histories. In a
24 study of salinity tolerance, crabs were held unfed at salinities of 5–50 (25 control) for up to 30 d.
25 Based on survivorship curves, *P. maclaughlinae* tolerated acute exposure to salinities of 10–45
26 for up to 18 d, and survivorship up to 30 d at 20–45 equaled or exceeded survivorship of the
27 control. In a study of acclimation, the osmotic pressure of hemolymph was measured after crabs
28 were held in the laboratory for 12, 48, and 96 h acutely exposed to salinities of 10–45. Paired *t*-
29 tests revealed that the crabs weakly hyperregulated their hemolymph at 45–154 mOsmol above
30 the external medium at all salinities and sampling times, and the osmotic differential of their
31 hemolymph was fully acclimated by 96 h. In a third study, acclimatization of hemolymph was
32 studied on crabs at 4 field sites that differed in their recent salinity histories. Field-collected
33 crabs weakly regulated their hemolymph 72–84 mOsmol above the external medium at all sites
34 sampled. Performance did not differ by site. The range of salinity tolerance and acclimation of
35 hemolymph of *P. maclaughlinae* partly explain their wide distribution, and the consistent
36 osmotic differential of its hemolymph indicates that the osmoregulatory ability of this small-
37 bodied species is conserved in populations throughout the lagoon. Although some other larger-
38 bodied hermit species in the region are euryhaline as adults, their tendency to hyperregulate
39 strongly at low salinities possibly adds an energetic burden that, along with their less euryhaline
40 long-lived larvae, might exclude them from the lagoon. Salinity tolerance of larval *P.*
41 *maclaughlinae* has yet to be studied.

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4	43
5	Key Words: distribution, ecology, osmoregulation, Paguroidea, physiology
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8	Regional Index Terms: USA, Florida, Indian River Lagoon
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66 1. Introduction

67 The Indian River Lagoon System is a complex of three lagoons (Mosquito Lagoon, Banana
68 River Lagoon, Indian River Lagoon). The system extends 250 km along the east coast of Florida
69 (U.S.A.), from Ponce de Leon Inlet at its northern end southward to Jupiter Inlet (Swain et al.,
70 1995). Its watershed is bounded on the east by dunes of the barrier islands and on the west by
71 the Atlantic Coastal Ridge and unnatural drainage basins (Woodward-Clyde Consultants, 1994).
72 This watershed is expanding due to human population growth, and the associated developments
73 in infrastructure, agriculture, and navigation have altered the circulation, water quality, and
74 landscape of the Indian River Lagoon System (De Freese, 1991; Woodward-Clyde Consultants,
75 1994; Kim et al., 2002; Duncan et al., 2004).

76 Although the lagoonal system has historically been polyhaline (Gilmore, 1995), with
77 wide ranges of salinity seasonally under the influences of precipitation, runoff, and evaporation
78 (Sheng et al., 1990; Sumner and Belaineh, 2005), salinities in recent decades have tended to
79 remain low for extended periods in the northern part of the system (Woodward-Clyde
80 Consultants, 1994). Changes in seagrass cover and associated macrobiota have been attributed
81 to these altered conditions (Dawes et al., 1995; Kensley et al., 1995; Nelson, 1995; Schmalzer,
82 1995). Changes in biota are not surprising given that estuarine communities are largely
83 composed of marine species whose populations extend into the estuary from nearby waters
84 (Remane, 1971). Because of their wide variation in environmental factors, estuaries are
85 physiologically stressful ecosystems for their inhabitants; and alterations in the historical
86 hydrology of estuaries only add to that stress. Consequently, Buzas and Hayek (2000) have
87 called for long-term monitoring of biota of the Indian River Lagoon System.

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4 88 One of the most common members of the decapod crustacean fauna of the lagoonal
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6 89 system is the small hermit crab *Pagurus maclaughlinae* García-Gómez, 1982 (Grizzle, 1974;
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9 90 Tunberg et al., 1994), an epiphyte grazer in seagrass beds (Smith, 1988.; Tunberg et al., 1994)
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11 91 with a warm-temperate Caribbean distribution (Raz-Guzman et al., Reported shield lengths of
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13 92 this hermit rarely exceed 3 mm (García-Gómez, 1982; Lemaitre et al., 1982; Tunberg et al.,
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16 93 1994; present study). There are more than a dozen species of hermit in the region belonging to
17
18 94 the genera *Calcinus*, *Clibanarius*, *Coenobita*, *Dardanus*, *Paguristes*, *Pagurus*, and *Petrochirus*
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20 95 (*Provenzano*, 1959; Grizzle, 1974; Camp et al., 1977; Gore et al., 1981;
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22
23 96 <http://www.sms.si.edu/irlspec/index.htm>), but *Pagurus maclaughlinae* is the only species found
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25 97 throughout the lagoons (Grizzle, 1974; Tunberg et al., 1994; Kelly and Turner, 2001). This
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27 98 hermit crab might, therefore, be adapted physiologically to the variable conditions of this
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29 99 lagoonal system differently than other hermits. Little work has been done on this species of
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31
32 100 hermit crab due to its relatively recent description as a species and frequent misidentification as
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34 101 *P. bonairensis* Schmitt, 1936 or *P. annulipes* (Stimpson, 1860) (García-Gómez, 1982). Studies
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36 102 have included distribution (Grizzle, 1974; Kelly and Turner, 2001), population ecology (Smith,
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38 103 1988; Tunberg et al., 1994), use of gastropod shells (Gilchrist, 1982, 1984; Robbins, 1998;
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40 104 Robbins and Bell, 2004), and description of larval stages (McLaughlin and Gore, 1988).
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42 105 Physiological studies might help us understand the broad distribution and abundance of *P.*
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44 106 *maclaughlinae* in the Indian River Lagoon System and elsewhere (Raz-Guzman et al., 2004).
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46 107 The ability of *P. maclaughlinae* to regulate would be consistent with our general knowledge that
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48 108 brackish-water animals are regulators (Gilles, 1975). The Crustacea show a range of osmotic
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50 109 abilities from osmoconformity to strong osmoregulation (Hoar, 1983). Osmoregulation has,
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52 110 however, been studied less in hermit crabs than in other decapod crustaceans (Mantel and
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4 111 Farmer, 1983), although hermit crabs of the genera *Pagurus* (Young, 1979) and *Clibanarius*
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6 112 (Sweeney, 1973; Young, 1979; Sharp and Neff, 1980) have received some attention.
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9 113 The purposes of the present study were to examine the salinity tolerance of adult *P.*
10
11 114 *maclaughlinae* and their osmoregulatory abilities over the short and long term based on survival,
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13 115 acclimation (regulatory response in the laboratory), and acclimatization (regulatory response in
14
15 116 the field). Specifically, we hypothesized (a) that *P. maclaughlinae* would maintain high
16
17 117 survivorship within the normal range of lagoon salinity (20–35, Gilmore, 1995; 10–35,
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19 118 Woodward-Clyde Consultants, 1994), (b) that they would acclimate and be hyperosmotic at all
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21 119 salinities within their range of salinity tolerance when acutely exposed, and (c) that they would
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23 120 be hyperosmotic to lagoon water at sites throughout the lagoon despite the long-term history of
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25 121 salinity changes at the sites (that is, they would acclimatize to field conditions). Such a study of
26
27 122 a small estuarine hermit would add to our limited knowledge of anomuran physiological ecology
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29 123 and might reveal an adaptation that enables this hermit crab to inhabit lagoons while other
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31 124 species of hermit are restricted to inlets.
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41 126 **2. Materials and Methods**

42 43 127 *2.1 Salinity Tolerance: Survivorship*

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45 128 On 18 February 2006, adult *Pagurus maclaughlinae* ($n = 210$) were taken from the northern
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47 129 Indian River Lagoon near Titusville, Florida, along the north shore of the causeway of State
48
49 130 Road 406 (Fig. 1, Table 1). Crabs were collected by sweeping with a dip net in dense beds of
50
51 131 shoalgrass, *Halodule wrightii* Ascherson, 1868, about 4 m from shore and in dense mats of the
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53 132 green alga *Caulerpa prolifera* (Forsskål, 1775) J. V. Lamouroux, 1809 about 10 m from shore.
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4 133 Ambient salinity at the site was 23 (Practical Salinity Scale), measured with an optical
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6 134 refractometer (accuracy of ± 1).

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9 135 The animals were held in the laboratory at 25 for 1 wk in two 38-l aquaria with sandy
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11 136 lagoonal substratum and epiphytized shoalgrass, and every other day they were fed pieces of up
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14 137 to 10 frozen shrimp [*Palaemonetes pugio* Holthuis, 1949, *Farfantepenaeus duorarum*
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16 138 (Burkenroad, 1939)] but rarely more than the crabs could consume in 24 h. After the 1-wk
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19 139 adjustment period, the hermit crabs ($n = 20$ per salinity) were acutely exposed to 9 test salinities
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21 140 (5, 10, 15, 20, 30, 35, 40, 45, 50) and the control (adjustment) salinity (25). These animals were
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24 141 tested in their shells to avoid giving an incorrect assessment of the species' physiological
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26 142 abilities (Sherman and Eichrodt, 1982). Crabs were starved during the experimental period to
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29 143 minimize confounding factors. The trial chambers were 81 mm-diameter petri dishes, each with
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31 144 50 ml of water and 1 crab. Mean laboratory temperature was $24.5 \pm 0.8^\circ\text{C}$ (mean \pm SE). Water
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33 145 was changed every 3 d and monitored for salinity with an optical refractometer (accuracy of ± 1).

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36 146 Crabs were checked for mortality after 1, 2, 4, 6, 12, 24, 48, 72, and 96 h and were monitored
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38 147 daily thereafter until mortality in the control group reached 50%, a strong indication of stress
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41 148 from starvation. Some *P. maclaughlinae* hide in their gastropod shells when stressed, but they
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43 149 emerged from their shells within 1 min of being turned over (aperture up). To confirm mortality
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46 150 in the present experiment, the apex of the gastropod shell of an unresponsive animal was
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48 151 removed with a rotary grinder to extract the crab. This extraction technique rarely needed to be
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51 152 used during the experiment because dead crabs usually extended from the shell aperture.

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53 153 Survivorship statistics (SPSS 14.0) were used for this study. Kaplan-Meier survival
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55 154 curves were constructed. This method uses the product-limit formula to estimate survival
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58 155 probabilities, taking into account right censorship; that is, each subject is not followed until death
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4 156 (Kleinbaum, 1996). The non-parametric Mantel log-rank test was chosen to determine
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6 157 significance because this test is considered the most conservative of all χ^2 approximations
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9 158 (Elandt-Johnson and Johnson, 1980). This statistic is a non-linear regression that compares the
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12 159 survivorship curve of the control group to curves of the test groups.

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14 160 Shield length, a standard measure of size in hermit crabs, was measured upon death or at
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16 161 the end of the study for surviving crabs by ocular micrometer under a dissection microscope,
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19 162 with magnification adjusted to give a range of 8–17 micrometer units. Normality of
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21 163 measurements of shield length in each treatment was tested by a Shapiro-Wilk test, and equality
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23 164 of variances was tested by a Levene test (SPSS 14.0). The mean ranks of the shield lengths of
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25 165 treatment groups were compared with a Kruskal-Wallis test (SPSS 14.0). Analysis of shield
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28 166 lengths allowed a post-hoc evaluation of success in assigning crabs of different sizes to treatment
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31 167 and control groups to avoid the presumably confounding effects of size on physiological
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33 168 performance.

34 35 36 169 *2.2 Osmoregulation: Acclimation of Hemolymph*

37 170
38 171 Hermit crabs were collected from the site near Titusville (Fig. 1) once a week during March
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41 172 2006 and maintained in the laboratory for 1 wk at a salinity of 25 with feeding as in the first
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43 173 experiment. Ambient salinities were 23–25 on collection dates (Table 1). After the adjustment
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45 174 period for each of the 4 weekly collections of crabs, groups of crabs were exposed unfed to test
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48 175 salinities for up to 96 h, and the osmotic pressures (*II*) of the hemolymph and the external
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50 176 medium were measured. Hemolymph extracted from members of each group was pooled
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53 177 because of the small blood volume of *P. maclaughlinae*. The repetition of this part of the study
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55 178 over 4 consecutive weeks allowed for more efficient harvesting of crabs within a tight time
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58 179 schedule; for it was difficult to remove the small crabs unharmed from their gastropod shells for
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4 180 extraction of hemolymph. Because sampling was destructive, hemolymph could not be removed
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6 181 repeatedly from individuals. Shield length was measured as described above.
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9 182 The test salinities were 10, 15, 20, 30, 35, and 40, and the control was 25. During each of
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11 183 the 4 experimental runs, a group of 5 animals was held in a petri dish at a test salinity or at the
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13 184 control salinity. Water was changed in the petri dishes at 48 h. Hemolymph drawn from 3 of the
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15 185 5 animals in each group was pooled for a sample. At each salinity, 3 such groups of 5 animals
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17 186 were exposed, 1 group for each time of sampling (12, 48, 96 h); a fourth group of crabs was held
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19 187 in reserve in case mass mortality occurred in 1 of the other 3 petri dishes. At the time designated
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21 188 for each group, hemolymph was withdrawn from each of 3 crabs with a hypodermic needle
22
23 189 inserted dorsomedially into the pericardium or heart. Puncture of articular membranes of the
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25 190 limbs was not possible because of the small size of the crabs. Samples from the 3 crabs were
26
27 191 pooled; and osmotic pressure was measured on 10 μ l of pooled hemolymph with a Wescor 5520
28
29 192 vapor-pressure osmometer. In addition, 6 crabs were selected from the holding aquarium at 0 h
30
31 193 for extraction, pooling (3 crabs per pooled sample), and analysis of hemolymph; these 2 pooled
32
33 194 samples were the 0-h part of the (25) control group. Osmotic pressure also was measured on
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35 195 samples of water in each petri dish (external medium). The accuracy of the vapor-pressure
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37 196 osmometer was ± 3 mOsmol.
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45 197 The difference in osmotic pressures (ΔI) of hemolymph and the external medium was
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47 198 computed for each group of crabs. One-tailed paired-sample *t*-tests (Zar, 1999) were applied at
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49 199 nearly all salinities and times to the mean differences with the hypothesis that the mean
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51 200 differences would exceed 0 mOsmol. The hypothesis was tested with a non-parametric
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53 201 Wilcoxon signed-rank test for the few data sets that were not normally distributed. To test the
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55 202 hypothesis that experimental animals had acclimated after 96 h of exposure, mean ΔI s were
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4 203 compared with a Kruskal-Wallis test. Shield lengths among treatments were compared as
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6 204 described above.

9 205 *2.3 Osmoregulation: Acclimatization of Hemolymph*

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11 206 Four sites in the lagoon (Fig. 1, Table 1) were selected based on the availability of data on water
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14 207 quality for 2006 from the St. Johns River Water Management District to evaluate recent salinity
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16 208 history. At each site, 10 random samples of 5 crabs each (50 crabs total) were collected by dip
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19 209 net. The location of each sample was selected haphazardly by the blind throw of a small marker
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21 210 buoy within the seagrass bed. At the same location where a group of 5 crabs was collected, a
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24 211 sample of bottom water was collected and sealed for later analysis. Crabs were transported to
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26 212 the laboratory in ambient lagoon water. Hemolymph of 3 of the 5 crabs from each group was
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28
29 213 drawn immediately upon arrival in the laboratory, pooled, and analyzed as described above; and
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31 214 osmotic pressure of the corresponding sample of bottom water was measured. The difference in
32
33
34 215 osmotic pressures (ΔII) of each paired sample of hemolymph and lagoon water was calculated.
35
36 216 Shield length was measured by ocular micrometer and compared as described above.

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38 217 A one-tailed paired-sample *t*-test (SPSS 14.0) was applied to the mean ΔII at each site to
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41 218 test the ability of *Pagurus maclaughlinae* to hyperregulate. The effect of site on the ability of *P.*
42
43 219 *maclaughlinae* to regulate its hemolymph was tested (Kruskal-Wallis test; SPSS 14.0) using ΔII
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45
46 220 as the dependent variable and site as the independent variable. Shield lengths among sites were
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48 221 compared as described above.

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53 223 **3. Results**

55 224 *3.1 Salinity Tolerance: Survivorship*

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225 The survivorship curves (Fig. 2, 3) for crabs held at 5 and 50 were significantly different from
226 that of the control group, held at 25 ($P < 0.01$; Table 2). Crabs acutely exposed to 5 began to die
227 after only 6 h, and all were dead by 48 h; 50% mortality was estimated by interpolation (Fig. 2)
228 to have occurred at 16.8 h. Crabs held at 50 died almost as quickly as those at 5, with 50%
229 mortality observed at 24 h, but 100% mortality was not reached until 10 d of exposure (Fig. 3).

230 Survivorship was high in all other groups for almost 2 wk (Fig. 3), at which time groups
231 held at 10 and 15 began to die more rapidly. Fifty percent of crabs held at 10 were dead by 18 d,
232 and all had died by 28 d of exposure. The group held at 15 was estimated by interpolation to
233 have achieved 50% mortality by 24.8 d, and some survived to the termination of the study at 30
234 d. After 30 d at 25, the control group reached 50% mortality, our subjective criterion for the
235 onset of starvation and other confounding effects. Survivorship curves in the remaining
236 experimental groups, exposed to 20, 30, 35, 40, and 45, were not statistically different than that
237 of the control at 20, 35 and 45 ($P > 0.05$; Table 2); and the 30 ($P < 0.01$) and 40 ($P < 0.05$)
238 groups had statistically higher survivorship than the control.

239 Shield lengths of crabs used in the survivorship study did not differ significantly across
240 salinities (1.7 ± 0.02 mm; Kruskal-Wallis test, $H = 5.275$, $df = 9$, $P = 0.81$).

241 *3.2 Osmoregulation: Acclimation of Hemolymph*

242 Before exposure to experimental salinities (time = 0 h), hemolymph osmotic pressure of crabs in
243 the control group (25) exceeded the osmotic pressure of the external medium ($\Delta\Pi = +82 \pm 9.5$
244 mOsmol; mean \pm SE; Table 3). After exposure, hemolymph osmotic pressure tracked external
245 osmotic pressure, although there appeared to be some overcompensation at 30, 35, and 40 at 12 h
246 (Fig.4, 5A) but not with longer exposure (Fig. 5B, C). Over the salinity range of 10–40, paired t -
247 tests revealed that the hermit crabs weakly regulated at 45–154 mOsmol above the external

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4 248 medium depending on salinity and time sampled; that is, the mean difference (mean $\Delta\Pi$)
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7 249 between the hemolymph and the external medium was statistically greater than 0 mOsmol (Table
8
9 250 3). Because values for $\Delta\Pi$ from the group held at 15 for 96 h were not normally distributed
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11 251 (Shapiro-Wilk test, $W = 0.751$, $P < 0.05$), a Wilcoxon signed-rank test was applied; and this
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14 252 mean, too, was found to be statistically greater than 0 mOsmol (Table 3).

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16 253 Hermit crabs in the control group (25) and lower salinities (10, 15, 20) exhibited a narrow
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19 254 range of regulation at 12 h (mean $\Delta\Pi = +66$ to $+71$ mOsmol; Table 3, Fig. 5A). The magnitude
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21 255 of the difference between the hemolymph and the external medium remained relatively small
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23
24 256 (mean $\Delta\Pi = +45$ to $+71$ mOsmol) after 48 h and 96 h of exposure (Table 3, Fig. 5B, C).

25
26 257 Osmotic pressures of hemolymph in groups held at elevated salinities were proportionately
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29 258 higher (mean $\Delta\Pi = +109$ to $+154$ mOsmol; Table 3, Fig. 5A) at 12 h; but they became similar to
30
31 259 the other groups upon further exposure (mean $\Delta\Pi = +58$ to $+94$ mOsmol; Table 3, Fig. 5B, C).

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33 260 All crabs had acclimated by 96 h of exposure, for the osmotic differentials of the hemolymph of
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36 261 all experimental groups and of the control group were statistically identical (Kruskal-Wallis test,
37
38 262 $H = 0.085$, $P = 0.738$). The extra crabs held in reserve in this experiment were unused because
39
40
41 263 survivorship was high in all treatments.

42
43 264 Shield lengths of crabs in the acclimation experiment were not significantly different (2.0
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45
46 265 ± 0.02 mm; $H = 2.987$, $df = 6$, $P = 0.81$).

47 48 266 *3.3 Osmoregulation: Acclimatization of Hemolymph*

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50 267 Salinities at the 4 collection sites (Fig. 1) did not vary more than 5 between high and low values
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53 268 over the 2 wk prior to sampling at each site (Table 1), but the salinities at time of sampling of
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55 269 hemolymph among collection sites were different: 22 at Site 1 near Titusville; 17 at Sites 2 and
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58 270 3 along Pineda Causeway near Palm Shores (Indian River Lagoon) and South Patrick Shores

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4 271 (Banana River Lagoon); 32 at Site 4 south of Sebastian Inlet. Field-collected *Pagurus*
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6 272 *maclaughlinae* weakly hyperregulated at all sites sampled regardless of the salinity at the time of
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8
9 273 collection; that is, the mean difference in osmotic pressure (mean $\Delta\Pi$) between the hemolymph
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11 274 and the bottom water was statistically greater than 0 at each collection site (Table 4). The means
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14 275 for $\Delta\Pi$ at all sites were similar ($+76 \pm 1.4$ mOsmol; Kruskal-Wallis test, $H = 0.766$; $df = 3, 36$; P
15
16 276 = 0.86) regardless of the differences in salinities at all sites: Site 1, 22, mean $\Delta\Pi = +76$ mOsmol;
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19 277 Site 2, 17, mean $\Delta\Pi = +72$ mOsmol; Site 3, 17, mean $\Delta\Pi = +73$ mOsmol; Site 4, 32; mean $\Delta\Pi =$
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21 278 $+84$ mOsmol. The variances were not homogeneous (Levene test, $W = 37.714$, $P < 0.01$).

22
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24 279 Shield lengths differed significantly among crabs sampled at the 4 sites for the
25
26 280 acclimatization study ($H = 10.767$, $df = 3$, $P < 0.05$), but these differences were not robust
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28
29 281 enough to be detected with the Nemenyi test (Zar, 1999), a Tukey-like post-hoc test. The range
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31 282 of mean shield lengths among the 4 sites was 2.2–2.5 mm.

32 33 283 34 284 **4. Discussion**

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36
37 285 *Clibanarius vittatus* (Bosc, 1802) (Diogenidae) and *Pagurus maclaughlinae* (Paguridae) are the
38
39 286 2 most abundant species of hermit crab in the Indian River Lagoon System. *Clibanarius vittatus*
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41
42 287 is found near inlets, and *P. maclaughlinae* is found throughout the lagoon system (Grizzle, 1974;
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44 288 Tunberg et al., 1994; Kelly and Turner, 2001). Other species of hermit crab are rare and
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47 289 primarily found at Sebastian Inlet (Grizzle, 1974): *Pagurus longicarpus* Say, 1817, *Clibanarius*
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49 290 *antillensis* Stimpson, 1862, *Petrochirus diogenes* (Linnaeus, 1758). Salinity is one
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51
52 291 physiologically critical factor that contributes to environmental variability in the lagoon (Sumner
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54 292 and Belaine, 2005) and that controls the distribution of inhabitants of estuaries (Remane, 1971).
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57 293 Prior to this study, the salinity tolerance and osmoregulatory abilities were known for *C. vittatus*
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59 294 and *Pagurus longicarpus* but not for *P. maclaughlinae*. Studying the physiological ecology of
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4 295 the latter species might explain the success of this crab in maintaining its wide distribution
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6 296 throughout this estuarine system over the last 34 yr (Grizzle, 1974; Kelly and Turner, 2001).
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9 297 Because the Indian River Lagoon System is polyhaline, it was expected that *Pagurus*
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11 298 *maclaughlinae* would exhibit a wide range of salinity tolerance, matching the normal range of
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13 299 lagoonal salinity [that is, 20–35 (Gilmore, 1995) or 10–35 (Woodward-Clyde Consultants,
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15 300 1994)]. The tolerance range found in this study for *P. maclaughlinae* is broader than expected
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17 301 (10–45 based on the point of 50% mortality), matching the lower end but exceeding the upper
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19 302 end of reported normal salinity ranges of the system. The salinity tolerance of *P. maclaughlinae*
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21 303 partly explains the presence of this small-bodied species throughout the Indian River Lagoon
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23 304 System; but the wide ranges of salinity tolerance typical of other hermit crabs in the region
24
25 305 (Biggs and McDermott, 1973; Young, 1980) do not explain their restriction to inlets. Other
26
27 306 factors must be responsible for their distributional differences, and these factors might include
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29 307 larval salinity tolerance, life history, supply of empty gastropod shells, interaction of multiple
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31 308 environmental variables (e.g., salinity and temperature; Biggs and McDermott, 1973; Young,
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33 309 1980), and the energy requirements for different levels of osmotic regulation. Comparisons
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35 310 between the salinity tolerance range of our Indian River Lagoon populations and those of the
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37 311 populations inhabiting multiple coastal lagoons in the southwestern Gulf of Mexico might also
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39 312 explain the abundance and distribution of this hermit in some coastal lagoons and not others
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41 313 (Raz-Guzman et al., 2004).
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50 314 The results of the acclimation study indicate that the pattern of osmoregulation of *P.*
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52 315 *maclaughlinae* is relatively consistent over the short and long term regardless of salinity. After
53
54 316 96 h, *P. maclaughlinae* weakly hyperregulated (Mantel & Farmer, 1983) their hemolymph 45–87
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56 317 mOsmol above all salinities to which they were exposed in the laboratory. These animals are not
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4 318 hyperosmotic osmoconformers because the difference between the hemolymph and the external
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6 319 medium exceeds 5–40 mOsmol (Mantel and Farmer 1983). Over the longer term, *P.*
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9 320 *maclaughlinae* sampled from 4 different sites all weakly hyperregulated their hemolymph at 72–
10
11 321 84 mOsmol above ambient osmotic pressure regardless of salinity history. The salinity histories
12
13 322 of these sites over the past year overlap. The Titusville and Sebastian Inlet populations
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15 323 experienced similar salinity histories from January 2005 to April 2006 (Fig. 6A, D; Titusville,
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17 324 15.70–29.71; Sebastian Inlet, 16.14–33.32). The Palm Shores and South Patrick Shores
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19 325 populations also experienced similar salinity ranges over the same period (Fig. 6B, C; Palm
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21 326 Shores, 12.70–20.51; South Patrick Shores, 12.45–19.56). The mechanism by which these
22
23 327 hermit crabs regulate seems to be conserved among populations in the northern Indian River
24
25 328 Lagoon System. Because *P. maclaughlinae* acclimate within 96 h to acute exposure to reduced
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27 329 and elevated salinities in the laboratory, it is likely that hemolymph osmotic pressures in field
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29 330 populations closely parallel the relatively slowly changing salinities encountered by crabs during
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31 331 their annual life cycle (Tunberg et al., 1994).

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33 332 Both *Pagurus longicarpus* and *Clibanarius vittatus* have geographically variable
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35 333 responses of their hemolymph to salinity. *Pagurus maclaughlinae* is hyperosmotic at salinities
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37 334 from 10 to 40, in contrast to *P. longicarpus* [and *P. pollicaris* Say, 1817] from South Carolina,
38
39 335 which is isosmotic at salinities of 5–40 (Young, 1979). The osmotic differential for hemolymph
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41 336 of *P. maclaughlinae* is well below that reported in the literature for *P. longicarpus* from
42
43 337 Massachusetts (mean $\Delta\Pi = 200\text{--}450$ mOsmol; Sherman and Eichrodt, 1982), where this species
44
45 338 is, therefore, a stronger regulator. *Clibanarius vittatus* from South Carolina strongly
46
47 339 hyperregulate below salinities of 40 and are isosmotic at 40 (Young, 1979); *C. vittatus* from the
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49 340 Gulf Coast of Texas are strong hyperregulators at low salinities (5–20) and weak hyperregulators

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4 341 at higher salinities (25–50; Sharp and Neff, 1980); *C. vittatus* from Pensacola, Florida, are
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6 342 hyperosmotic at lower salinities (0–11) and hypoosmotic at higher salinities (25 and 44;
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9 343 Sweeney, 1973); on the Atlantic Coast of Florida, *C. vittatus* perform similarly to the Texas Gulf
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11 344 Coast population—strong hyperregulators at 15, weak hyperregulators at 40, and isosmotic at 35
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13 345 (Rhodes, 2006). The differences in results among Sweeney (1973), Young (1979), Sharp and
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15
16 346 Neff (1980), and Rhodes (2006) might be due partly to the salinity history of the crabs in the
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19 347 field. In addition, *C. vittatus* often an intertidal crab, is presumably faced with a broader range of
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21 348 temperature, salinity, and desiccation than the subtidal *P. longicarpus* (Young, 1979) and *P.*
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23 349 *maclaughlinae*.

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26 350 The potential mechanisms involved in crustacean osmoregulation are well known. In
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28
29 351 marine crustaceans, regulation consists of two essential processes: anisosmotic extracellular
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31 352 regulation and isosmotic intracellular regulation (Gilles, 1975). Hemolymph osmotic pressure is
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33 353 maintained by anisosmotic extracellular fluid regulation. Isosmotic intracellular regulation
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36 354 controls the solute concentration in cells (Gilles, 1975). Anisosmotic extracellular regulation is
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38 355 the response observed in the present study, for no cellular mechanisms were studied. Various
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41 356 organs and ion-transport mechanisms are likely to play roles in osmoregulation by *P.*
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43 357 *maclaughlinae*, but these were not the focus of this study. Future research on ionic regulation by
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46 358 *P. maclaughlinae* should be modeled after studies on other decapod crustaceans (for example,
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48 359 Sweeney, 1973; Charmantier et al., 1988; Schleich et al., 2001; Towle and Weihrauch, 2001; Lin
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50 360 et al., 2002; Vinagre et al., 2002; Kinsey and Lee, 2003).

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53 361 The energy required for an animal to maintain a strong hyperregulatory or
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55 362 hyporegulatory state is greater than that for an animal that is a weak regulator or for one that is
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58 363 isosmotic (Robertson, 1960; Lockwood, 1967). These differential energy requirements for
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4 364 different levels of osmoregulatory abilities might be another factor that explains the distribution
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7 365 of hermit crabs in the Indian River Lagoon System. *Clibanarius vittatus* is a stronger regulator
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9 366 at lower salinities than at higher salinities (Young, 1979; Sharp and Neff, 1980; Rhodes, 2006).
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11 367 This species must then expend more energy to live at low salinities and might select the inlets of
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13
14 368 the Indian River Lagoon System to minimize the energy spent on regulation and to maximize the
15
16 369 residual energy for other activities. *Pagurus maclaughlinae* maintain their weak regulatory state
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19 370 regardless of salinity and might not expend more energy over the long term at high or low
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21 371 salinities.
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26 373 **5. Conclusion**

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28 374 The broad salinity tolerance and consistent osmotic performance of *Pagurus maclaughlinae* over
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31 375 the short and long term give clues to how this species has evolved to thrive in the hydrologically
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33 376 variable Indian River Lagoon System. Future work on larval tolerance and on osmoregulatory
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36 377 mechanisms might further explain the distribution of this small-bodied lagoonal species in
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38 378 contrast to the restriction of other larger-bodied hermit crabs to the vicinity of inlets. This hermit
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41 379 is an epiphyte grazer in seagrass beds (Smith, 1988.; Tunberg et al., 1994), which are highly
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43 380 productive habitats that stabilize sediment, recycle nutrients, and form the basis of estuarine food
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46 381 webs (Williams and Heck, 2001). Loss of grazers and escalation of anthropogenic nutrient loads
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48 382 cause epiphytic algae on seagrass blades to increase in biomass, resulting in shading and
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51 383 subsequent decline in primary production of the seagrasses (Williams and Heck, 2001). Further
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53 384 work on the physiological tolerance of other grazers in the Indian River Lagoon System might be
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55 385 crucial to our understanding the effects of anthropogenic disturbances on the ecosystem. Not all
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58 386 might be as resilient as *P. maclaughlinae*.

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20 394
21 395 **7. References**

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26 530 **Figure Captions**

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28 531 Fig. 1. Collection sites for *Pagurus maclaughlinae* and water-quality stations (St. Johns River
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30 532 Water Management District) in the northern Indian River Lagoon System. See Table 1 for
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32 533 station data.

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36 534 Fig. 2. Short-term survivorship curves for *Pagurus maclaughlinae* held at salinities of 5, 10, 45,
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38 535 and 50. Survivorship of crabs held at other salinities was 100 through 96 h of exposure. $N = 20$
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40 536 crabs per group.

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43 537 Fig. 3. Long-term survivorship curves for *Pagurus maclaughlinae* held at all experimental
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45 538 salinities. Control group was held at 25. $N = 20$ crabs per group.

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48 539 Fig. 4. Time-related short-term response of hemolymph of *Pagurus maclaughlinae* exposed
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50 540 acutely to salinities of 10–40. Filled symbols and solid lines, osmotic pressure (IT) of
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52 541 hemolymph; open symbols and dashed lines, osmotic pressure of external medium. $N = 4$ pooled
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54 542 samples (3 crabs each) per mean except for 0 h ($n = 8$).

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4 543 Fig. 5. Salinity-related short-term response of hemolymph of *Pagurus maclaughlinae* exposed
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6 544 acutely to salinities of 10–40. A, after 12 h exposure. B, after 48 h exposure. C, after 96 h
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8 545 exposure. The diagonal line from the origin is the isosmotic line. Nominal salinities of exposure
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10 546 are given above each mean in B. Standard errors are given for osmotic pressures of both the
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12 547 hemolymph and the external medium if error bars exceed the width of symbols. $N = 4$ pooled
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14 548 samples (3 crabs each) per mean.

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19 549 Fig. 6. Long-term trends in salinity in the northern Indian River Lagoon System, January 2005
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21 550 to April 2006. A, Titusville. B, Palm Shores. C, South Patrick Shores. D, Sebastian Inlet.
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23 551 Refer to Fig. 1 for locations of sites. Source: St. Johns River Water Management District (L.
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25 552 Hall and W. Tweedale, personal communication).

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31 554 **Tables**

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33 555 Table 1. Station data. Numbers in left column signify collecting sites, and letters signify nearby
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35 556 St. Johns River Water Management District water-quality monitoring stations (Fig. 1). Dates on
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37 557 which crabs were collected for the acclimatization study are indicated by the dagger (†).

Site	Coordinates	Date	Salinity
1, Titusville	28° 37' 22" N	18 Feb 06	23
	80° 48' 32" W	03 Mar 06	23
		12 Mar 06	23
		17 Mar 06	23
		24 Mar 06	25

			31 Mar 06†	22
2, Palm Shores	28° 12' 31" N		18 Feb 06	17
	80° 39' 19" W		29 Mar 06	12
			05 Apr 06	14
			11 Apr 06	16
			18 Apr 06†	17
3, South Patrick Shores	28° 12' 22" N		29 Mar 06	13
	80° 38' 06" W		05 Apr 06	13
			11 Apr 06†	16
4, Sebastian Inlet	27° 50' 25" N		26 Mar 06	36
	80° 26' 00" W		21 Apr 06	34
			09 Apr 06†	35
A, Titusville	28° 38' 09" N		15 Feb 06	20.58
	80° 48' 07" W		14 Mar 06	22.59
			18 Apr 06	26.69
B, Palm Shores	28° 11' 40" N		13 Feb 06	14.84
	80° 38' 56" W		13 Mar 06	15.04
			17 Apr 06	18.51
C, South Patrick Shores	28° 11' 56" N		14 Feb 06	14.57
	80° 37' 32" W		16 Mar 06	15.36
			19 Apr 06	17.42
D, Sebastian Inlet	27° 47' 48" N		21 Feb 06	29.75
	80° 26' 56" W		20 Mar 06	29.01

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4 560 Table 2. Statistical comparison of survivorship curves for *Pagurus maclaughlinae* exposed
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7 561 acutely to salinities of 5–50 for 30 d. The curve of each experimental group ($n = 20$) was
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9 562 compared to that of the control group (25). Survivorship curves are given in Fig. 2 and 3.
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Salinity	Mantel Log-rank (χ^2)	P
5	41.577	< 0.01
10	21.207	< 0.01
15	4.729	< 0.05
20	2.840	0.09
25	—	—
30	7.110	< 0.01
35	0.586	0.44
40	6.238	< 0.05
45	0.793	0.37
50	43.868	< 0.01

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4 565 Table 3. Differences between osmotic pressures of hemolymph and external medium for
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6 566 *Pagurus maclaughlinae* exposed acutely to salinities of 10–40. Mean values are accompanied by
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9 567 standard errors and are compared to 0 mOsmol by *t*-tests, except for the group held at 15‰ for
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11 568 96 h; data for the latter were not normally distributed and were compared by the Wilcoxon
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14 569 signed-rank test (*z*). *, significant at $P < 0.05$; **, significant at $P < 0.01$; $n = 8$ pooled samples
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16 570 (3 crabs per sample) for the control (25) at 0 h; $n = 4$ for other means.
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Salinity	Osmotic Pressure Differential (mOsmol) at:			
	0 h	12 h	48 h	96 h
10		+77 ± 12.2	+51 ± 13.0	+57 ± 16.7
		6.305**	3.915*	3.390*
15		+71 ± 14.8	+67 ± 17.6	+45 ± 5.6
		4.792**	3.810*	1.841*
20		+69 ± 14.6	+71 ± 18.5	+47 ± 25.6
		4.717**	3.831*	3.785*
25	+82 ± 9.5	+66 ± 13.9	+48 ± 3.2	+58 ± 11.6
	8.618**	4.770**	14.487**	4.978**
30		+154 ± 28.9	+65 ± 6.7	+58 ± 19.4
		5.352**	9.730**	2.988*
35		+147 ± 21.3	+82 ± 18.9	+62 ± 12.9
		6.881**	4.316*	4.777**
40		+109 ± 33.1	+94 ± 29.9	+87 ± 28.6

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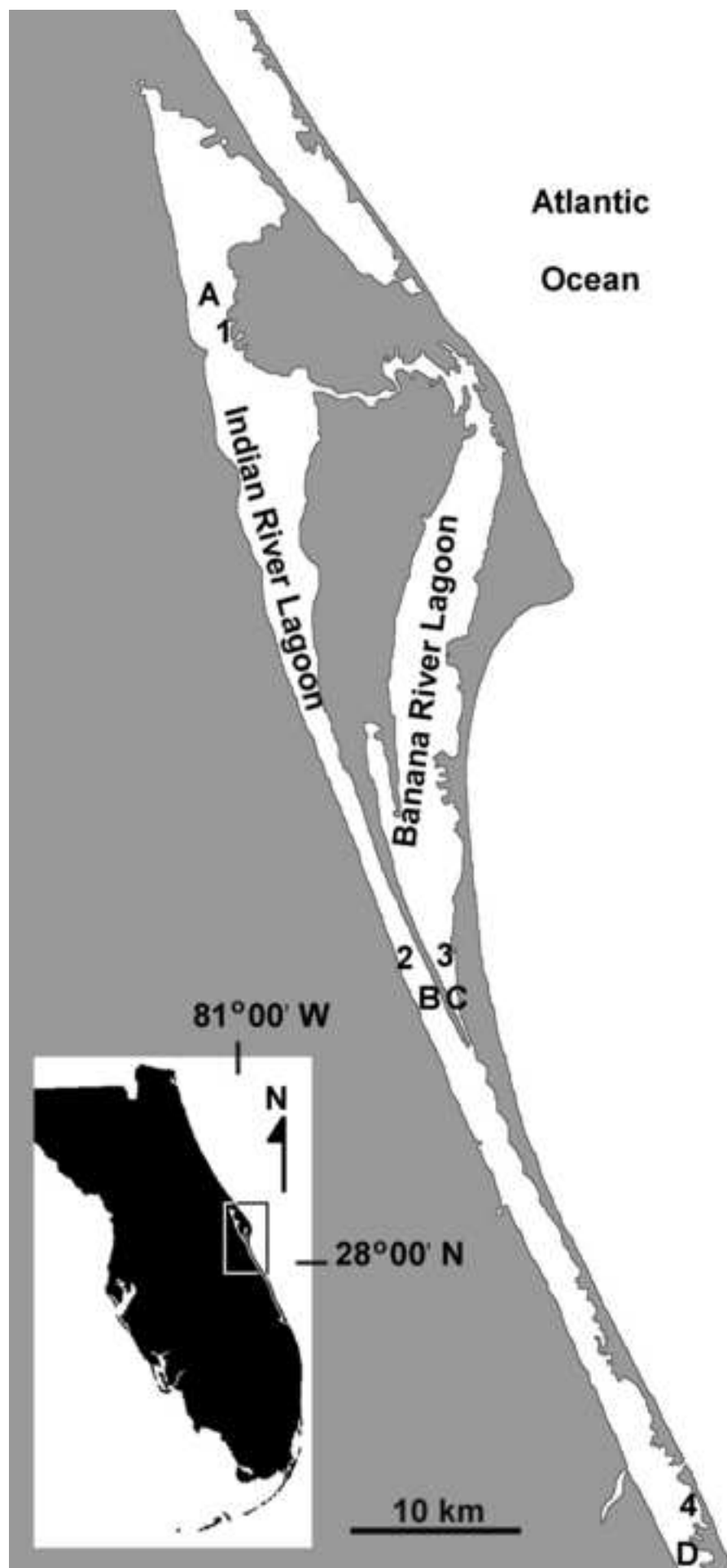
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4 574 Table 4. Osmotic pressure of lagoon water and of hemolymph of acclimatized *Pagurus*
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6 575 *maclaughlinae* from 4 sites in the Indian River Lagoon System. At each site, osmotic pressure
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9 576 (*II*) was measured in 10 samples of bottom water and in 10 pooled samples of hemolymph from
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11 577 3 crabs per sample. See Fig. 1 and Table 1 for location of sites and for selected environmental
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14 578 conditions. *, $\Delta II > 0$ mOsmol at $P < 0.05$.

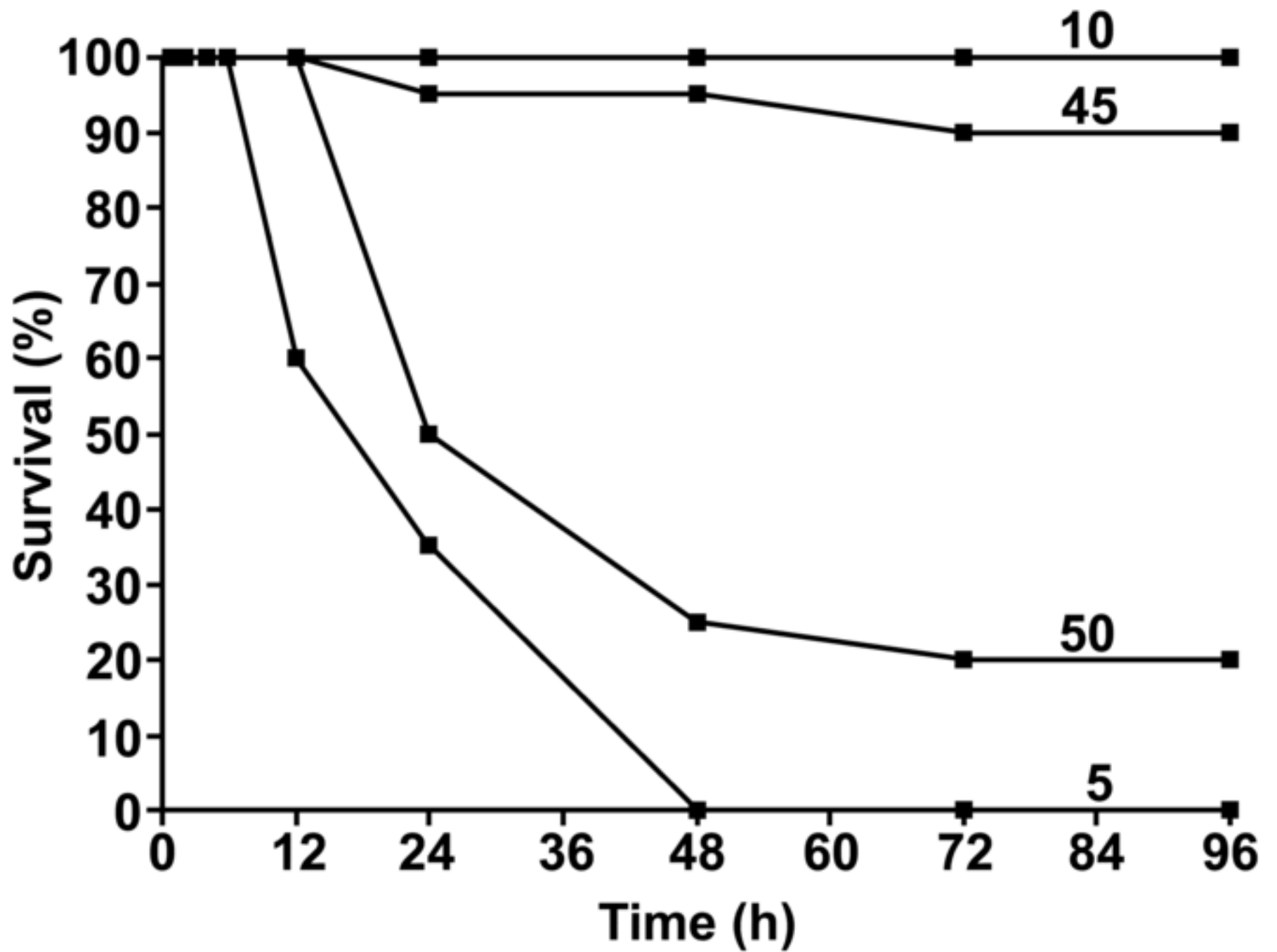
Site	Osmotic Pressure (mOsmol)		
	Hemolymph (mean \pm SE)	Bottom Water (mean \pm SE)	ΔII (mean \pm SE)
1, Titusville	818 \pm 5.8	742 \pm 2.3	76 \pm 6.0*
2, Palm Shores	593 \pm 7.5	521 \pm 0.9	72 \pm 5.3*
3, South Patrick Shores	561 \pm 3.9	487 \pm 1.4	73 \pm 3.9*
4, Sebastian Inlet	1061 \pm 5.6	977 \pm 2.8	84 \pm 8.2*

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Figure(s)

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