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The effects of temperature and salinity on molting and survival of *Menippe adina* and *M. mercenaria* (Crustacea, Decapoda) postsettlement juveniles

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ABSTRACT: Comparing the effects of temperature and salinity on the survival and growth of animals in early life stages may contribute toward our understanding of the basic ecological differences between congeneric species and of the evolutionary mechanisms operating within a genus. Postsettlement juvenile crabs of the species *Menippe adina* and *M. mercenaria* were held in factorial arrays of temperature and salinity to determine the effects of these factors on survival and molt frequency. The patterns of the effects of temperature and salinity on both molting and survival were similar for the 2 species. Optimal conditions predicted for survival of each species were also similar, but the percentage of crabs that survived at specific treatments differed. In general, *M. adina* showed a greater tolerance to low temperature and low salinity than did *M. mercenaria*. The observed differences may be important in determining the distribution of these species in terms of both their geographical range and their distribution from nearshore to offshore. These differences may be species-specific, with some adaptation to local conditions; species-specific differences would support a theory of allopatric speciation of these *Menippe* species.

INTRODUCTION

The physical parameters to which a species is exposed have a significant impact on its physiology. The most common environmental factors used to test physiological response of marine organisms are temperature and salinity, and a comparison of responses to these factors can help determine if fundamental ecological differences exist between 2 congeneric species. Different responses to temperature and salinity have been found for congeneric marine species in areas such as kinetic properties of enzymes (Hochachka & Somero 1984), energetics (Levinton 1983), oxygen compensation (Mangum 1963), and osmoregulation (Rodriguez 1981). The most basic responses that can be used to compare species are survival and growth (i.e. development). These responses may reflect or influence other aspects of biology such as distribution, reproduction, and behavior.

Studies of differences in the effects of temperature and salinity on survival and growth of animals in early life stages are especially important because animals at these stages are usually more sensitive to environmental parameters than are adults (Kinne 1970, 1971). Watts et al. (1982) found that rates of larval development differed between sibling species of *Echinaster* when temperature and salinity differed. Mills & Fish (1980) determined that *Corophium arenarium* could not penetrate as far upstream in an estuary as *C. volutator* because *C. arenarium* juveniles were less tolerant of low salinity. Similarly, Antonopoulou & Emson (1989) suggested that temperature and salinity tolerance limits prevent *Palaemonetes longirostris* larvae from inhabiting the upper parts of estuaries where *P. varians* larvae can develop. In brachyurans, the postsettlement juvenile stage represents an interesting period in the life cycle: crabs have entered the benthic habitat but have not yet developed adult tolerances to physical factors (Kinne 1970, 1971).

In the Gulf of Mexico, 2 species of stone crab occur: *Menippe adina* in the western portion, and *M. mercenaria* in the eastern portion. Along the coast of northwest Florida, the ranges of these species overlap and hybrid forms, as well as pure species, have been identified based on phenotypic and genotypic characteristics (Bert & Harrison 1988). Throughout the range, *M. mercenaria* typically live in burrows in grass flats or in crevices among rocks and experience annual temperatures and salinities that are relatively stable (Bert et al. 1986). *M. adina* also live among oyster reefs and mud flats in areas where temperature and salinity fluctuate seasonally (Baltz & Horst 1992).

Survival and development of larvae held in the laboratory at various temperature-salinity combinations have been reported for both *Menippe mercenaria* (Ong & Costlow 1970, Field 1989, Brown et al. 1992) and *M. adina* (Field 1989). In comparing these species, Field (1989) used only 2 temperature levels, so differences in the effects of temperature are unclear, but she used 5 salinity levels. She concluded that at low salinities, a higher proportion of *M. adina* larvae survived than did *M. mercenaria* larvae; however, *M. mercenaria* developed faster at all salinities than did *M. adina*. Trigg et al. (1989) compared survival of adult [>60 mm carapace width (CW)] *M. adina* and *M. mercenaria* at 4 temperatures and 4 salinities. They found that adult *M. adina* have a greater ability to tolerate combinations of low temperatures and low salinities, whereas adult *M. mercenaria* are better able to tolerate combinations of high temperatures and high salinities.

Understanding the physiology of postsettlement juvenile *Menippe* (those ≤10 mm CW) is important because crabs may remain in this size class for a full year (Tweedale et al. 1993) and therefore experience the annual range of temperature and salinity. Brown et al. (1992) studied the influence that these factors had on the survival and molting of postsettlement juvenile *M. mercenaria* in the laboratory. The present study examined the effects of temperature and salinity on both *M. adina* and *M. mercenaria* postsettlement juveniles over 2 years, allowing us to compare the responses between the 2 species and between years within a species. Our work promotes further understanding of the ecological differences between these species and of how these differences may be related to evolution within the genus.

MATERIALS AND METHODS

Menippe adina juveniles ≤10 mm CW were obtained from Mississippi Sound, Mississippi, during September 1990 (n = 269) and October 1991 (n = 415). Crabs were collected from mesh bags of oyster shell that had been suspended subtidally from channel markers. Juvenile *M. mercenaria* were collected from Tampa Bay, Florida, during October 1989 (n = 304) and June 1991 (n = 271), from the outside of commercial stone crab traps. Size of the juveniles ranged from 1.7 to 10.4 mm CW; at least 90 % of juveniles from each data set were between 2.3 and 9.4 mm CW.

In the laboratory, juveniles were held for 42 d in a factorial array of either 7 or 8 temperatures (5 to 35 °C, or 5 to 40 °C, 5 °C increments) and 7 salinities (10 to 40 ‰, 5 ‰ increments). These treatments were selected to include the range of conditions that juveniles would experience in their natural environment. For each treatment, 5 to 10 crabs were held separately in 100 to 150 ml of artificial seawater, in either refrigerated incubators (5 to 20 °C and 40 °C treatments) or temperature-controlled water baths (20 to 35 °C treatments). Crabs were first acclimated to the experimental temperatures at a rate of 2 °C per day, then acclimated to the experimental salinities at a rate of 2 ‰ every 2 to 3 h. Each day of both the acclimation and experimental periods, juveniles were checked for molting activity or mortality; except for the days of salinity acclimation, crabs were fed minced conch every other day and placed in clean water of the appropriate temperature and salinity on the alternate day. Temperature was recorded daily and salinity was measured during the water change. The mean temperatures and salinities measured during the experiments varied no more than 0.4 °C and 0.7 ‰, respectively, from the predetermined experimental values.

For each species, the proportion of juveniles molting during the experimental period (molting) and the proportion of juveniles surviving to the end of the experimental period (survival) were compared between years using the R × C *G*-test of independence (Sokal & Rohlf 1981). Because we found significant differences between years in both molting ($p < 0.001$) and survival ($p < 0.001$) for *Menippe adina*, each data set was treated separately. We found no significant difference in molting or in survival between the 2 years for *M. mercenaria*; therefore, we pooled the data sets for all analyses. No juveniles of either species that were held in 40 °C water survived beyond the acclimation period; thus, the temperature range for all analyses was 5 to 35 °C.

For each data set (1990 *Menippe adina*, 1991 *M. adina*, and *M. mercenaria*), the percentage of juveniles that survived in each treatment was square-root transformed and fitted to a response-surface regression (SAS Institute, Inc. 1985). The effects of temperature (*T*) and salinity (*S*) on response (*R*, molting or survival) were analyzed using the nonparametric 3-way log-linear model (3-way *G*-test; Sokal & Rohlf 1981). Step I of this test determined if a 3-factor interaction existed among *T*, *S* and *R*; if a significant *G*-value ($p \leq 0.025$) resulted from this step, the R × C *G*-test was performed between pairs of factors ($T \times R$, $S \times R$) at each level of the third factor. Each R × C *G*-test was followed by the simultaneous test procedure for homogeneity of frequencies (STP; Sokal & Rohlf 1981) to determine at which treatments differences in response occurred. If step I of the 3-way *G*-test was not significant, we proceeded to step II, which tested for independent interactions between *T* and *R* and between *S* and *R*. For each pair of factors found to have a significant 2-factor interaction ($p \leq 0.025$) in step II, we performed the STP over pooled values of the third factor to further define *T* and *S* effects. Steps III and IV of the 3-way *G*-test were not necessary for any of our analyses. Survival interval, defined as the proportion of the experimental period during which a crab remained alive, was calculated for each treatment with 100 % mortality. The effect of *T* or *S* on mean survival interval was analyzed using the R × C *G*-test and the STP.

We compared molting, survival, and mean survival interval of *Menippe mercenaria* to that of 1990 *M. adina*; because both overall survival and molting of 1991 *M. adina* were significantly lower than that of either 1990 *M. adina* or *M. mercenaria*, no further comparisons were made using the 1991 *M. adina* data set. Three-way *G*-tests were performed using the factors *T*, *R*, and species (*M*) at each *S* and using the factors *S*, *R*, and *M* at each *T*. In this case, a nonsignificant result at step I determined that no 3-factor interaction existed and therefore that the effect of *T* or of *S* on *R* did not differ between the species. At step II, 2-factor interactions were not tested between *T* or *S* and *M* because these factors were all fixed by the experiment; 2-factor interactions were also not examined between *T* or *S* and *R* because we had already performed these tests for each species separately and were not interested in the effects of *T* and *S* on both species combined. The remaining test at step II, between *M* and *R*, determined whether a response differed between *M. adina* and *M. mercenaria* at each *T* or *S* level. When a significant difference was found, we performed R × C *G*-tests between *M* and *R* at each temperature-salinity combination that was included in that *T* or *S* level. For each treatment in which all juveniles of both species died, we compared mean survival intervals between species using the R × C *G*-test.

RESULTS

Molting

For 1990 *Menippe adina*, the highest proportion of juveniles (83 %) molted in water of 25 °C, 20‰ and 30 °C, 15‰; for 1991 *M. adina*, the highest proportion of juveniles (78 %) molted in water of 30 °C, 20‰. In both data sets, the only significant interactions were the 2-factor interactions between *T* and molting ($p < 0.001$). A number of crabs molted in water of 20 to 35 °C, but few or no crabs molted in water of 5 to 15 °C (Table 1).

The percentage of *Menippe mercenaria* that molted was highest (83 %) in water of 20 °C, 25‰. In this species too, *T*, but not *S*, significantly affected molting ($p < 0.001$). A moderate-to-high percentage of juveniles molted in 20 to 30 °C water, a low percentage of juveniles molted in 15 and 35 °C water, and no juveniles molted in 5 to 10 °C water (Table 1).

When the species were compared at each *S* level, the *G*-values for the 3-factor interactions among *T*, *M*, and molting were not significant. The absence of 3-factor interactions indicates that neither the magnitude nor the direction of the effect of *T* differed between the species. In both species, molting was very low or nonexistent from 5 to 15 °C, increased from 20 to 30 °C, then decreased at 35 °C (Fig. 1).

Table 1. *Menippe* spp. Homogeneous sets of temperature levels for the proportion of postsettlement juveniles that molted (pooled salinities). Temperatures are ordered, left to right, from lowest to highest percentage of crabs that molted (shown in parentheses). Underlined groups of temperatures did not have significantly different molt frequencies (simultaneous test procedure for homogeneity of frequencies)

Data set	Temperature (°C), % of crabs molted						
M. adina, 1990[a]	5 (0)	10 (2)	15 (3)	20 (27)	35 (37)	25 (47)	30 (55)
M. adina, 1991[b]	5 (0)	10 (0)	15 (1)	35 (6)	20 (21)	25 (23)	30 (36)
M. mercenaria, 1989 and 1991, combined[c]	5 (0)	10 (0)	15 (6)	35 (18)	20 (30)	25 (44)	30 (49)

[a] n ranged from 39 to 44 ($\bar{x} = 42$); [b] n ranged from 62 to 70 ($\bar{x} = 67$); [c] n ranged from 79 to 108 ($\bar{x} = 88$)

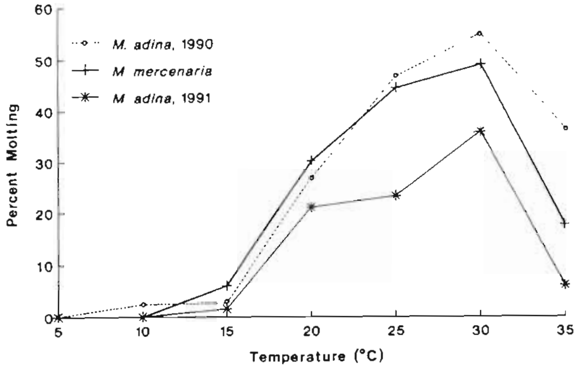

Fig. 1. *Menippe* spp. Percentage of postsettlement juveniles that molted at each temperature level tested (pooled salinities)

Survival

One hundred percent of *Menippe adina* survived in the following treatments: 1990 – 15 °C and 20, 25, 35 or 40‰; 20 °C and 15 to 35‰; 30 °C and 30 or 35‰; 1991 - 20 °C and 25‰. Although overall survival was lower for 1991 *M. adina* than for 1990 *M. adina*, response-surface regressions predicted optimal survival at similar conditions for each data set; highest survival of 1990 *M. adina* was predicted at 23 °C, 33‰ ($r^2 = 0.74$, $p < 0.001$), and highest survival of 1991 *M. adina* was predicted at 21 °C, 33‰ ($r^2 = 0.64$, $p < 0.001$). For 1990 *M. adina*, a significant 3-factor interaction existed among *T*, *S*, and survival ($p < 0.001$). High proportions of juveniles survived in water of 15 to 30 °C and 20 to 40‰ (Table 2); at *T* levels near the optimum temperature, survival was very high over a wide range of *S*, and at high *T* levels, survival was highest at high *S*. For 1991 *M. adina*, *T* and *S* affected survival independently (each factor: $p < 0.001$). Survival was low at extreme *T* levels (5 and 35 °C) but generally increased as *T* approached the optimum; survival at all salinities above 20‰ was relatively high (Table 2).

Survival of *Menippe mercenaria* was 100 % in water of 15 °C and 25 or 35‰; 20 °C and 30 to 40‰; 25 °C and 35‰. Optimal survival of juveniles was predicted by the response-surface regression at 22 °C, 32‰ ($r^2 = 0.81$, $p < 0.001$). Independently, *T* and *S* significantly affected survival (each factor: $p < 0.001$); comparatively high survival was observed at the 15 to 30 °C levels and at the 20 to 40‰ levels (Table 2).

When *Menippe mercenaria* survival was compared to 1990 *M. adina* survival, no significant 3-factor interactions were found among *T*, *M*, and survival or among *S*, *M*, and survival. Again, the lack of interactions indicates that the patterns of the *T* and *S* responses were the same for both species. Two-factor interactions between *M* and survival were significant at the 20 °C ($p = 0.015$) and 15‰ ($p = 0.012$) levels (Fig. 2), and in both cases survival of *M. adina* was higher than survival of *M. mercenaria*.

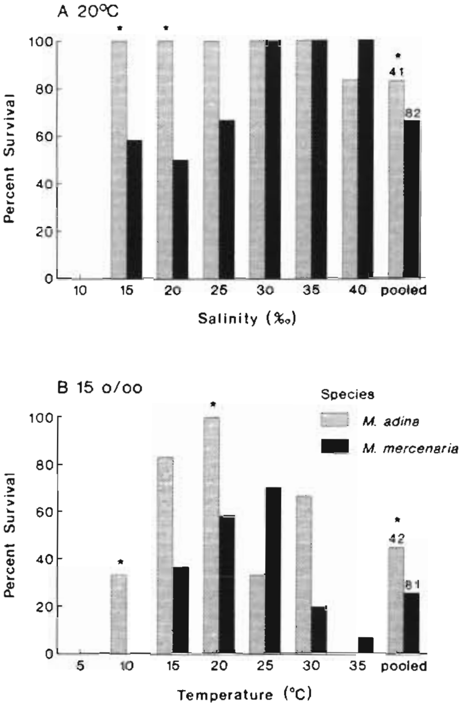

Fig. 2. *Menippe* spp. Percentage of postsettlement juveniles that survived at factor levels where significant differences between species were found. (A) 20 °C, (B) 15‰. *Treatments where survival of *M. adina* was significantly greater than that of *M. mercenaria* (p ranged from 0.018 to 0.035). Sample size ranges for each cell: *M. adina*, 1990: 5 to 7; *M. mercenaria*, 1989 and 1991 combined: 10 to 15. Pooled n is shown above the bar for each species

Survival interval

For 1990 *Menippe adina*, mean survival interval at 5 °C generally increased significantly with each *S* increment; at 10‰, mean survival interval was significantly shorter at 5 °C than at other *T* values and increased with *T* through 30 °C (Fig. 3A). Shortest mean survival interval of 1991 *M. adina* was at combinations of extreme *T* (5 or 35 °C) and low *S* (10‰) (Fig. 3B). Mean survival interval of *M. mercenaria* held at combinations of low *S* (10 to 15‰) and either low or extremely high *T* (5, 10, and 35 °C) was significantly shorter than mean survival interval of juveniles held at low levels of one factor and intermediate or high levels of the alternate factor (Fig. 3C).

No juveniles of either 1990 *Menippe adina* or *M. mercenaria* survived to the end of the experiment at any treatment including 10‰ or at the treatments of 5 °C, 15 to 30‰. Mean survival interval differed sig-

Table 2. *Menippe* spp. Homogeneous sets of treatments for the proportion of postsettlement juveniles that survived. Treatments are ordered, left to right, from lowest to highest percentage of crabs that survived (shown in parentheses). Underlined groups of treatments did not have significantly different survival (simultaneous test procedure for homogeneity of frequencies)

***M. adina* 1990** [a]

Salinity (‰)	Temperature (°C), % survival						
10	5 (0)	10 (0)	15 (0)	20 (0)	25 (0)	30 (0)	35 (0)
15	5 (0)	35 (0)	10 (33)	25 (33)	30 (67)	15 (83)	20 (100)
20	5 (0)	10 (17)	35 (50)	30 (67)	25 (83)	15 (100)	20 (100)
25	5 (0)	35 (50)	10 (67)	25 (67)	30 (83)	15 (100)	20 (100)
30	5 (0)	10 (17)	25 (50)	15 (67)	35 (67)	20 (100)	30 (100)
35	5 (17)	10 (50)	35 (50)	25 (67)	15 (100)	20 (100)	30 (100)
40	5 (20)	10 (67)	25 (67)	35 (67)	20 (83)	30 (83)	15 (100)

Temperature (°C)	Salinity (‰), % survival						
5	10 (0)	15 (0)	20 (0)	25 (0)	30 (0)	35 (17)	40 (20)
10	10 (0)	20 (17)	30 (17)	15 (33)	35 (50)	25 (67)	40 (67)
15	10 (0)	30 (67)	15 (83)	20 (100)	25 (100)	35 (100)	40 (100)
20	10 (0)	40 (83)	15 (100)	20 (100)	25 (100)	30 (100)	35 (100)
25	10 (0)	15 (33)	30 (50)	25 (67)	35 (67)	40 (67)	20 (83)
30	10 (0)	15 (67)	20 (67)	25 (83)	40 (83)	30 (100)	35 (100)
35	10 (0)	15 (0)	20 (50)	25 (50)	35 (50)	30 (67)	40 (67)

***M. adina* 1991, pooled values** [b]

Temperature (°C), % survival						
5 (0)	35 (9)	10 (23)	25 (33)	30 (39)	15 (43)	20 (52)

Salinity (‰), % survival						
10 (0)	15 (9)	20 (26)	30 (37)	35 (38)	40 (42)	25 (46)

***M. mercenaria* 1989 and 1991, pooled values** [c]

Temperature (°C), % survival						
5 (0)	35 (28)	10 (29)	30 (49)	20 (67)	15 (69)	25 (71)

Salinity (‰), % survival						
10 (2)	15 (26)	20 (40)	40 (51)	25 (59)	35 (61)	30 (62)

[a] n ranged from 5 to 7; [b] n ranged from 62 to 69 ($\bar{x} = 66$); [c] n ranged from 76 to 105 ($\bar{x} = 84$)

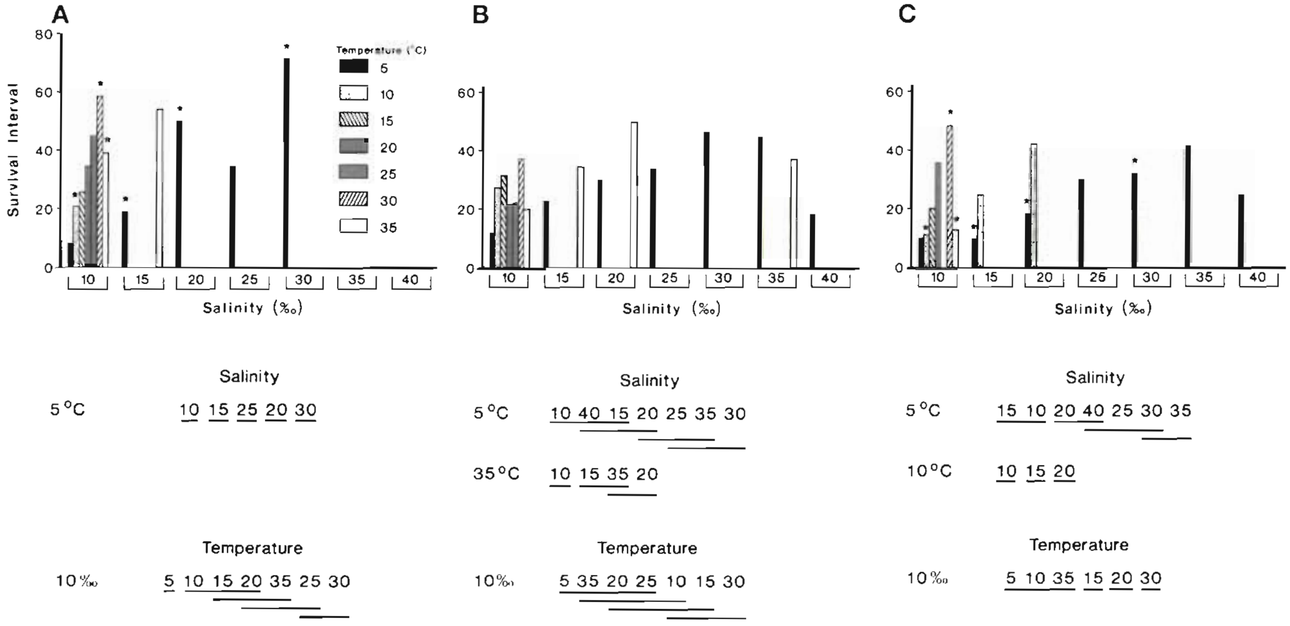

Fig. 3. *Menippe* spp. Mean survival interval (percentage of the experimental period that crabs lived) of postsettlement juveniles at treatments with 100 % mortality. (A) *M. adina*, 1990. (B) *M. adina*, 1991. (C) *M. mercenaria*, 1989 and 1991 combined. Groupings below histograms show homogeneous sets of temperatures and salinities for each data set. Treatments are ordered, left to right, from lowest to highest mean survival interval. Underlined groups of treatments did not have significantly different mean survival intervals (simultaneous test procedure for homogeneity of frequencies). *Treatments where mean survival interval of *M. adina* was significantly greater than that of *M. mercenaria* (p ranged from <0.001 to 0.009)

nificantly between species at several of these treatments (see asterisks in Fig. 3); at each treatment, mean survival interval of *M. adina* was significantly longer than mean survival interval of *M. mercenaria*. In general, treatments that included 10 °C and low or moderate *S* (10 to 20 ‰) were lethal to *M. mercenaria*, but only 10 °C, 10 ‰ was lethal to *M. adina* (Fig. 3). In both species, juveniles held in 10 ‰ water survived longest at 30 °C, and juveniles held in 5 °C water survived longest at 30 to 35 ‰.

DISCUSSION

Differences in overall survival between *Menippe adina* juveniles collected in 1990 and in 1991 may have been the result of unusual hydrological conditions in Mississippi Sound in 1991. During May of that year, salinities declined to less than 10 ‰ and did not increase until mid-July (Gulf Coast Research Laboratory, Ocean Springs, MS, USA, unpubl. data). No ovigerous females were observed in the Sound until August (H. M. Perry pers. comm.), so virtually all of the juveniles in our study would have hatched from eggs spawned within 1 mo after salinities began to increase. The low salinity during that period may have negatively affected the gravid or ovigerous females, the embryos, or the larvae. This result supports the idea that annual differences in temperatures and salinities can greatly influence overall survival within a species. Nevertheless, the patterns of the temperature and salinity effects were similar and the optimal conditions predicted for survival were nearly identical for the 2 groups, indicating that the effects of temperature and salinity are constant from year to year.

The similarity between *Menippe adina* and *M. mercenaria* in the relatively low temperature predicted for optimal survival is not surprising; the operation of natural selection should be such that each species would have evolved so that survival was highest when juveniles were most abundant. In both Mississippi Sound and Tampa Bay, highest numbers of postsettlement juveniles have been collected when temperatures are decreasing from summer highs of approximately 30 °C to values around 25 °C (Stuck & Perry 1992, Bert unpubl. data). The low temperature values for optimal survival may also be based on physiology. The hemocyanin-oxygen transport system in adult *M. mercenaria* works most efficiently at 15 °C, and an increase to 25 °C decreases oxygenation to about 50 % (Mauro & Mangum 1982).

The patterns of the effects of temperature and salinity on molting were similar for both *Menippe adina* and *M. mercenaria*; the proportion of juveniles that molted was very low in 5 to 15 °C water, increased with water temperature to 30 °C, and then decreased in 35 °C water. Although the effects of temperature on molt frequency of juveniles did not differ between species, annual growth rates in nature may differ between the 2 populations we sampled because mean high and low temperatures and the lengths of the seasons vary latitudinally. In Tampa Bay, water temperatures typically are 30 °C or higher during July and August and are 20 °C or lower from December through February (Fig. 4). In Mississippi Sound, water temperatures may reach 30 °C only during September, if at all, and typically are less than 20 °C from December through April (Fig. 4). Because molt frequency declines as temperature decreases below 30 °C and virtually ceases below 20 °C, juveniles from the population farther south may have a longer annual growth period.

High proportions of juveniles of both species survived in water of 15 to 30 °C and 20 to 40‰; nevertheless, we found significant differences between *Menippe mercenaria* and 1990 *M. adina* in the proportion of juveniles that survived at specific temperature and salinity levels. Both high and low levels of temperature and salinity influenced juvenile survival, but we saw the strongest evidence of a difference between species near the lower ends of their tolerance ranges. Juveniles of neither species showed a significant decrease in survival with increased salinity, but the upper temperature limit for survival was between 35 and 40 °C for both *M. mercenaria* and *M. adina*. Because water temperatures rarely exceed 35 °C in most parts of the species range, juveniles would seldom encounter temperatures too high for survival. Alternatively, a significantly higher proportion of *M. adina* survived than did *M. mercenaria* at several treatments that included both low salinities and low to intermediate temperatures. In addition, *M. adina* survived in 5 °C water if salinity was high, but *M. mercenaria* did not. A low-salinity threshold for both species was evident between 10 and 15‰; however, survival intervals calculated from our data showed that when held in water of 30 °C, *M. adina* survived approximately 4 wk at 10‰, significantly longer than *M. mercenaria* survived. Thus, *M. adina* appear to tolerate a broader range of naturally occurring temperatures and salinities than do *M. mercenaria*, allowing them to better survive variation on both a spatial and a temporal scale.

Tolerance limits of a species in the early life stages may be critical in determining its distribution. For most organisms, tolerance to environmental extremes increases with ontogeny (Kinne 1970, 1971), and this appears to be true for both species of *Menippe*. The limits of temperature tolerance for *M. adina* larvae are unclear from previous work, but low-temperature tolerances of larvae and postsettlement juveniles may define the northern limit of the species' range for *M. mercenaria* (Brown et al. 1992). Tolerance to salinity, on the other hand, may help determine the location of a population in relation to the coast (see e.g. Mills & Fish 1980, Steele & Steele 1991). Because *M. adina* juveniles have a greater tolerance to low salinities, this species may be able to inhabit nearshore areas that are not tolerated by *M. mercenaria* in early stages of the life cycle.

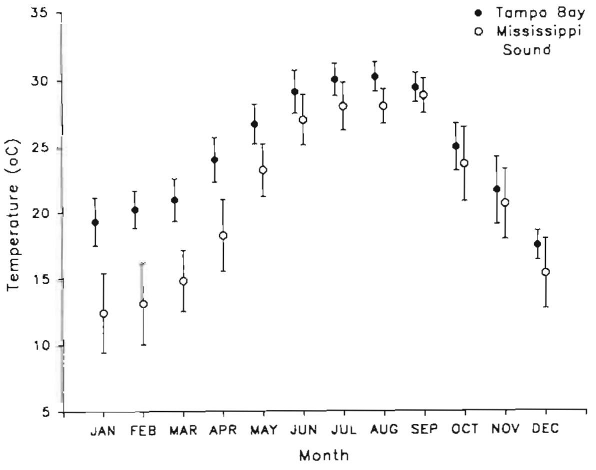

Fig. 4. Mean monthly temperatures (± SD): Mississippi Sound, Mississippi, USA, December 1973 to February 1992 (Gulf Coast Research Laboratory, Ocean Springs, MS, unpubl. data); Tampa Bay, Florida, USA, May 1988 to December 1992 (Hillsborough County Environmental Protection Commission, Tampa, FL, unpubl. data)

Differences in temperature or salinity tolerances between 2 populations may be due to 3 reasons (Kinne 1962): acclimatization, irreversible non-genetic compensation, or genetic differences. We acclimated the juveniles to the test temperatures and salinities, thus eliminating any acclimatization that had already taken place. Because they had been spawned no more than 2 mo before collection, the juveniles used in our comparative analyses had experienced very little variation, either as eggs or as larvae, from the temperatures and salinities at which they were collected. These temperatures and salinities were similar for both 1990 *Menippe adina* and *M. mercenaria*, so non-genetic compensation was also unlikely. Thus, the differences we see must have a genetic basis. An important question remains: Are these differences species-specific, or are they the result of heritable, local adaptation? Examples can be found of genetic differences in the temperature responses of organisms among populations both within and between species, even over relatively short latitudinal distances

(2 to 5°). Populations of *Crassostrea virginica* from Massachusetts/Long Island and New Jersey/Virginia required different temperatures for spawning even after a 2 yr acclimation (Loosanoff & Nomejko 1951). Differences in survival and growth of *Ophryotrocha costlowi* and *O. macrovifera* held at various temperatures persisted for 10 generations (Levinton 1983).

From our data we cannot determine whether the different temperature tolerances of *Menippe adina* and *M. mercenaria* are due to genetic differences between species or to adaptation to local conditions, but a combination seems probable. When viewed in conjunction with field studies, the differences that we observed in salinity tolerances seem to be species-specific, but the differences in response to temperature may be a combination of species-specific differences and within-species adaptation. Throughout the species' ranges, *M. adina* is found in lower salinity waters than is *M. mercenaria* (see Sullivan 1979, Bert et al. 1986, Landry 1992, Stuck & Perry 1992); in the zone of hybridization, *M. adina* is more common nearshore where salinity is lower and more variable, but both species occur offshore (Wilber 1992, Bert unpubl. data). Furthermore, despite the similar salinity conditions to which the juveniles used in our species comparison were exposed prior to collection, juvenile *M. adina* exhibited higher survival in low salinity water, particularly in low-salinity/low-temperature combinations. In contrast, the temperature ranges experienced overall by the 2 species in nature are similar because the latitudinal range of *M. mercenaria* spans that of *M. adina* (Williams & Felder 1986). Still, our juvenile *M. adina* had a greater ability to survive in low temperatures. As with the lengths of the growth and reproductive seasons, which are presumed to be strongly influenced by temperature (Bert et al. 1986, Brown et al. 1992) and vary inversely with latitude, this tolerance may be the result of adaptation to conditions at the location of collection. Nevertheless, some species-specific adaptation toward an overall broader temperature tolerance in *M. adina* is likely, because the estuarine waters occupied by *M. adina* typically exhibit greater temperature fluctuations than do more oceanic waters.

A total or partial species-specific difference in tolerances to temperature and salinity supports the scenario for the divergence of *Menippe mercenaria* and *M. adina* proposed by Bert (1986). She suggested that the terminal Miocene glaciation caused sufficient reduction in the range of the ancestral species and alteration of major oceanic current flow as to cause a decrease in gene flow between populations in the eastern and western Gulf of Mexico and Caribbean Sea. While the 2 populations were separated, each would have inhabited regions with different physical attributes; adaptations of each population to its environment may have resulted in a divergence in tolerances to environmental factors. After subsequent range expansion and secondary contact by the populations, each newly diverged form would have remained essentially in different types of environments: *M. mercenaria* would have occupied areas with more stable temperatures and marine salinities, and *M. adina* would have occurred in areas with larger annual variations in temperature and salinity. The distributional patterns of the species and the partial habitat partitioning in the zone of hybridization that we see today suggest that selection is continuing to promote those physiological differences developed initially in allopatry.

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