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Salinity Tolerance of Four Ecologically Distinct Species of *Fundulus* (Pisces: Fundulidae) from the Northern Gulf of Mexico

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SALINITY TOLERANCE OF FOUR ECOLOGICALLY DISTINCT SPECIES OF *FUNDULUS* (PISCES: FUNDULIDAE) FROM THE NORTHERN GULF OF MEXICO.—Fishes that use estuaries during all or a portion of their life history provide an ideal opportunity to study the influence of abiotic factors on distribution and abundance as they relate to the highly variable conditions in that environment. Often, closely related species segregate along

abiotic estuarine gradients (see Martin, 1988; Dunson et al., 1993), and this is most obvious when congeneric species exhibit species-specific salinity tolerances. One of the most abundant groups of estuarine resident fishes in the Western Hemisphere are members of the Fundulidae, with 28 species in the genus *Fundulus*. By nature, this group is extremely euryhaline (Nordlie and Walsh, 1989; Porschbacher et al., 1990; Toepfer and Barton, 1992), but has been found to segregate along salinity gradients (Weisberg, 1986; Peterson and Ross, 1991).

Our understanding of the relationship between salinity and fundulid occurrence and abundance stems mainly from distributional studies, although photoperiod has been shown to affect salinity selection/preference in *F. grandis* (Fivizzani and Meier, 1978; Spieler et al., 1976). *Fundulus grandis* occurs between 0.1 and 76.0 (Simpson and Gunter, 1956; Renfro, 1960), *F. m. similis* between 0.8 and 76.1‰ (Kilby, 1955; Simpson and Gunter, 1956), *F. chrysotus* between 0 and 24.7‰ (Kilby, 1955), and *F. notti* between 0 and 10.0‰ (Peterson and Ross, 1991). Because a more accurate understanding of estuarine community assembly requires quantification of the direct effects of salinity, we became interested in salinity tolerance of fundulids. Specifically, we wanted to determine the salinity tolerance of four fundulids that distribute themselves along salinity gradients, which, in our area, range from 0 to ~28‰. To achieve this, we quantified acute (7‰, 14‰, 21‰, 28‰, and 35‰) and chronic (salinities up to 70‰) salinity exposures for *F. notti* and *F. chrysotus*, two species that use tidal freshwater and oligohaline sections of the Biloxi Bay estuary, MS, and *F. grandis* and *F. m. similis*, two euryhaline fundulids found lower in the estuary.

Materials and methods.—Field collections and laboratory adjustment protocols: The four species of fundulids were collected from Biloxi Bay and Old Fort Bayou, MS, and transported to the laboratory in water from the collection site between October and November. These postspawning fundulids (Greeley et al., 1986, 1988) ranged between 30 and 50 mm total length (TL), and we used both male and female fish in the experiments. The fish were left in coolers with high aeration overnight to allow the water to adjust to room temperature. Fish were then transferred to holding tanks with salinities equal to those in which they were caught (salinities varied depending on location and date collected). *Fundulus chrysotus* and *F. notti* were held at 0‰. Preliminary data

TABLE 1. Mean percent survival of fundulids acutely exposed to five salinity treatments after being adjusted to 0‰ (*F. notti* and *F. chrysotus*) or 3‰ (*F. grandis* and *F. m. similis*).

Salinity (‰)	<i>F. notti</i>	<i>F. chrysotus</i>	<i>F. grandis</i>	<i>F. m. similis</i>
7	100	100	100	100
14	88	100	100	100
21	0	91	100	100
28	0	24	100	100
35	0	0	100	100

indicated that *F. m. similis* died in freshwater conditions; thus, *F. m. similis* and *F. grandis* were adjusted to ~3‰ by exchanging aerated freshwater with the water in the holding tank such that the salinity dropped 5‰ per day until ~3‰ was reached. These species were allowed an additional 2 d to adjust to ~3‰. All holding and experimental tanks were kept at 25 ± 2 C. We maintained the photoperiod at a 12L:12D cycle to mimic the natural cycle at the time of collection, and because of its influence on the neuroendocrine system and, thus, salinity tolerance in *Fundulus* (Fivizzani and Meier, 1978; Spieler et al., 1976). Collection and adjustment procedures were identical for both acute and chronic experiments.

Acute salinity experiments: For the acute-exposure experiments, twenty 19-l aquaria were placed into circulating water baths and randomly assigned a salinity (7‰, 14‰, 21‰, 28‰, or 35‰) by species ($n = 4$) combination. Five fish of each species were acutely transferred into the aquaria from holding tanks (salinity = 0‰ or ~3‰) so that each species was exposed to each salinity. One 96-hr run contained one replicate of every species/salinity combination and was considered to be one block. A total of four blocks were run sequentially. The 96-hr runs began at 0800 hr, and during the first 24 hr, the fish were checked at 1, 3, 6, and 9 hr. On subsequent days, fish were checked at 0800 and 1700 hr until 96 hr elapsed. We used probit analysis, a statistical procedure to estimate the salinity at which 50% of the test organisms died, to calculate a 96-hr LC_{50} for salinity (SPSS Version 6.1, 1994). A one-way analysis of variance (ANOVA) in a randomized complete block design was used to test for differences among the 96-hr LC_{50} means calculated by the probit analysis of the four species.

Chronic salinity experiments: For the chronic-exposure experiments, twenty-four 19-l aquaria containing freshwater or water of low (3‰)

salinity were placed into circulating water baths and randomly assigned a treatment combination (species by experimental or species by control condition; three replicates each). Five fish of each species were randomly placed into each of the three replicate experimental and control aquaria. Salinity was increased from 0‰ or 3‰ to 5‰ (species dependent) and then increased by 5‰/d for 14 d in the experimental tanks by adding synthetic sea salts (Forty Fathoms Biocrystals Marine Mix). Fish that survived at 70‰ were held for 24 hr and then removed and measured as noted above. Control tanks remained at the initial salinity (0‰ or 3‰) for 14 d.

Results.—Over the range of salinities in the acute tests, no individuals of *F. m. similis* or *F. grandis* died (Table 1). However, some *F. chrysotus* and *F. notti* died upon acute transfer; the mean 96-hr LC_{50} of *F. chrysotus* was 25.6‰, and the mean 96-hr LC_{50} of *F. notti* was 17.0‰ (Table 1). There was no significant block effect ($F = 0.79$; $df = 3$; $P = 0.573$), so data were pooled and analyzed with a one-way ANOVA. The difference in 96-hr LC_{50} means between *F. chrysotus* and *F. notti* was significant ($P = 0.0036$; Table 2).

Even with slow adjustment, all *F. notti* in the experimental tanks died at 144 hr at a salinity of 30‰ (Fig. 1A); no control *F. notti* died. All experimental *F. chrysotus* survived salinity increases up to 40‰ and exhibited a slightly reduced survival rate up to 55‰ (Fig. 1A). Mortality markedly increased after 60‰, with no survival at 70‰. No control *F. chrysotus* died. In contrast, *F. grandis* mortality slowly increased throughout the entire experiment in both control (80.0% survival) and experimental (73.3% survival) tanks (Fig. 1B). The same general pattern of salinity tolerance was exhibited for control (76.7% survival) and experimental (73.3% survival) *F. m. similis* (Fig. 1B).

Discussion.—One of the most intriguing and productive areas of research focuses on the relationship between abiotic and biotic factors

TABLE 2. ANOVA summary table for acute salinity tolerance experiments for *F. notti* and *F. chrysotus*. In the original analysis, replicates were blocked across time, and no significant block effect was found ($F = 0.79$; $df = 3$; $P = 0.573$), so data were pooled and analyzed with a one-way ANOVA.

Source	df	Sum of squares	Mean square	F statistic	P value
Main effect	1	148.781	148.781	21.334	0.0036
Error	6	41.844	6.974		
Total	7	190.625			

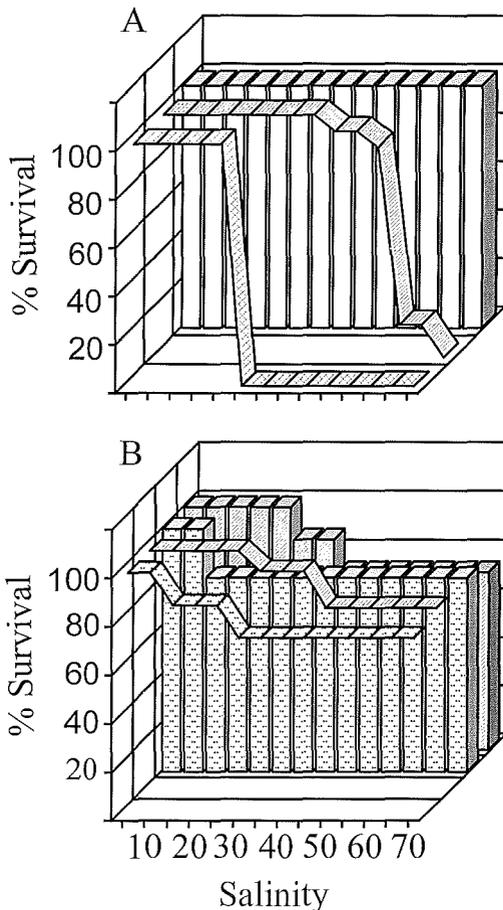


Fig. 1. Percent survival of (A) *Fundulus notti* and *F. chrysotus* and (B) *F. grandis* and *F. m. similis* exposed to sequentially increasing salinity treatments ($n = 14$) over a 14-d period. The "open" histogram in panel A represents the controls of both species, which were 100%. The slashed line represents data for *F. notti* and the checked line represents *F. chrysotus*. In panel B, the slashed histogram represents the controls for *F. m. similis*, whereas the dotted histogram represents controls for *F. grandis*. The lines represent the treatment data and shades match between the histogram and line data.

and how they relate to community structure. In estuarine systems, salinity is an abiotic factor influencing distribution and abundance, as well as growth and reproduction, of metazoans (Barnes, 1967; Martin, 1988; Dunson et al., 1993). In our study, we demonstrated that four of the more abundant fundulids found in the Biloxi Bay estuarine system had different salinity tolerances. *Fundulus grandis* and *F. m. similis* tolerated slow salinity increases up to 70‰, compared to *F. notti* and *F. chrysotus*, which tolerated salinities up to only 15‰ and 55‰, respectively. *Fundulus chrysotus* is clearly more salt-tolerant than is *F. notti* and has been shown to occur in brackish waters (Springer and Woodburn, 1960; Peterson and Ross, 1991). For example, although Peterson and Ross (1991) collected both *F. notti* and *F. chrysotus* in brackish waters, 99.1% of *F. notti* occurred in tidal freshwater habitats (0.9 ± 0.4 salinity; mean \pm SE) and 91.7% of *F. chrysotus* occurred in oligohaline habitats (4.0 ± 0.9 salinity). Data from this study show that survival was higher for fishes slowly acclimated to increasing salinity than for those acutely exposed. Furthermore, slow-acclimation data are comparable to maximum-salinity data from the literature (Gunter, 1945; Kilby, 1955; Simpson and Gunter, 1956; Springer and Woodburn, 1960; Forman, 1968; Griffith, 1974; Peterson and Ross, 1991) for all four species. Thus, slow acclimation appears to be more relevant to understanding ecological differences between species than are data from acute-exposure experiments.

The fundulids examined in this study are not found everywhere along the estuarine salinity gradient in our system, which ranges from 0‰ to ~ 28 ‰, nor are they found over the range that our tests suggest they can tolerate. Numerous species of cyprinodontids and fundulids, regardless of their present habitats, retain significant adaptive characteristics of euryhalinity (Nordlie and Walsh, 1989; Toepfer and Barton, 1992). Our data also suggest that salinity by itself does not influence *F. grandis* and *F. m. similis* as much as it influences *F. notti*

and *F. chryсотus* and that the former two species should be able to use habitats along the entire salinity gradient. Gunter (1945) and Simpson and Gunter (1956) also concluded that salinity did not limit the distribution of *F. m. similis* and *F. grandis*, although they reported that *F. m. similis* was found mainly when salinity was $>20\%$, while *F. grandis* was collected from a wider range of salinities, including lower-salinity waters. Thus, some other factor(s), in conjunction with salinity, appear to influence estuarine distributional pattern (Peterson and Ross, 1991; pers. obs.).

Barnes (1967), working with a series of crabs, noted that habitat, rather than optimal physiological responses, may be the ultimate determiner of species distribution within their range of tolerated salinities. It is possible, then, that habitat features in conjunction with salinity are playing a role in the distribution of *F. m. similis* and *F. grandis*. For example, *F. m. similis* prefers shallow, soft, sandy bottom habitats (Gunter, 1945; Reid, 1954; Kilby, 1955; Springer and Woodburn, 1960; Forman, 1968; Martin and Finucane, 1968; Relyea, 1983) to muddy bottoms. Springer and Woodburn (1960) and Martin and Finucane (1968) noted that *F. m. similis* burrow into sandy bottoms when threatened by a predator. In contrast, *F. grandis* occasionally is found in shallow beach habitats (Reid, 1954; Forman, 1968; Relyea, 1983), but prefers muddy flats and bayous (Gunter, 1945; Forman, 1968; Springer and Woodburn, 1960; Subrahmanyam and Drake, 1975; Relyea, 1983), where they are more abundant. Kilby (1955) noted that *F. grandis* is "more responsive to the type of habitat than to salinity, provided that salinity is at least brackish and not $>25\%$." Future research needs to focus on the interaction of salinity and habitat choice in determining distribution of *Fundulus* along the estuarine gradient.

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