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## Ontogenetic Changes in Behavioral and Energetic Responses of Juvenile Atlantic Croaker (*Micropogonias undulatus*) to an Estuarine Salinity Gradient

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### Abstract

Larval Atlantic croakers (*Micropogonias undulatus*) ingress into estuaries from offshore spawning sites during fall and winter. Larvae and early juveniles migrate up-estuary to oligohaline nurseries where they reside for several months before emigrating seaward. We examined ontogenetic changes in behavioral salinity preference and avoidance as potential contributors to these movement patterns along the estuarine salinity gradient. Four size classes (26-40, 41-55, 56-70, and 71-85 mm standard length) were acclimated to 10‰ and 18°C, and exposed to horizontal salinity gradients providing five discrete salinity choices: 2, 6, 10, 14, and 18‰. Behavioral salinity preference varied ontogenetically: 26-40 mm

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24 juveniles avoided salinities  $\leq 10\text{‰}$  and preferred higher salinities, 41-55 mm juveniles showed a shift  
25 toward lower salinities, and 56-70 mm fish continued this trend by preferring 2‰ and avoiding 18‰.  
26 The largest fish tested (71-85 mm) showed no significant preference or avoidance behavior, although  
27 they tended to avoid the low and prefer the high salinities tested. Preference for higher salinities  
28 among early (26-40 mm) juveniles may facilitate orientation in higher-salinity bottom waters, assisting  
29 up-estuary immigration to oligohaline nurseries via residual bottom layer inflow. Low salinity  
30 preference by 56-70 mm juveniles is consistent with their residence in oligohaline areas. We also  
31 conducted feeding and growth experiments, at 18°C, on 30-40 mm and 75-85 mm fish, corresponding to  
32 the smallest and largest fish in the salinity preference trials. Smaller juveniles showed no significant  
33 energetic advantage in oligohaline versus mesohaline conditions. However, larger juveniles grew  
34 significantly faster at 18‰ than 2‰, indicating that movement down-estuary during summer and fall  
35 improves growth capacity later in the nursery season. Increased precipitation and river discharge  
36 predicted from climate change, and associated stronger net up-estuary flow of saline bottom waters,  
37 may facilitate up-estuary immigration of early juvenile Atlantic croakers through their attraction to  
38 higher salinity demonstrated by the present work.

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## 42 INTRODUCTION

43 Seasonal and ontogenetic migrations between habitats are common life history strategies of  
44 marine and estuarine fishes (Secor 2015). Migrations are especially pronounced for many oceanic  
45 spawners whose larvae then immigrate to estuaries where they exhibit temporally and spatially complex  
46 patterns of estuarine residency and movement (Able and Fahay 1998). Migrations are presumed to  
47 enhance the fitness of individuals by placing them in habitats most conducive to growth and/or survival  
48 at each life stage (Roff 1988). Although migrations are often temporally and spatially predictable, the  
49 specific cues that trigger them are not well described for many species (Smith 2012; Secor 2015).

50 For transient species whose larvae and juveniles traverse wide estuarine salinity gradients  
51 during their nursery phase, salinity is a potentially important cue for 1) orientation during estuarine  
52 ingress/egress, and 2) behavioral selection of particular nursery zones during estuarine residency (Serafy

53 et al. 1997; Secor 2015). The seasonal timing of estuarine movements such as immigration and  
54 emigration may be influenced by ontogenetic changes in salinity preference and/or energetic responses  
55 to salinity gradients (Moser and Gerry 1989; Bernatzeder et al. 2010; Ern et al. 2014).

56 The Atlantic croaker (*Micropogonias undulatus*), a member of the ecologically and economically  
57 important family Sciaenidae, is abundant along the U.S. Atlantic coast from Cape Cod, Massachusetts to  
58 southern Florida, and along the Gulf of Mexico coast as far south as Campeche Bay, Mexico. Atlantic  
59 croakers support important commercial and recreational fisheries, particularly within the U.S. Mid-  
60 Atlantic Bight (MAB) from North Carolina to New Jersey (ASMFC 1987). Atlantic croakers spawn over  
61 the southern MAB continental shelf beginning in late summer and increasing during fall and early winter  
62 (Able and Fahay 1998, 2010). Larvae ingress into estuaries during the fall and winter (Warlen 1982;  
63 Witting et al. 1999; Ribeiro et al. 2015) and are transported up-estuary during their transformation into  
64 juveniles. They aggregate as young juveniles in oligohaline nursery areas for 4 to 8 months (Miller et al.  
65 2003). Emigration down-estuary from oligohaline areas begins as size-specific 'bleeding off' (Yakupzack  
66 et al. 1977) of larger (>70 mm standard length) juveniles to deeper, more saline habitats during summer  
67 (Moser and Gerry 1989), followed by a mass exodus when water temperatures decrease in the fall  
68 (Nelson 1969; Weinstein 1979; Miglarese et al. 1982; Miller 1985; Miller and Able 2002; Miller et al.  
69 2003; Hare and Able 2007).

70 Here we employed laboratory experiments to investigate ontogenetic changes in the behavioral  
71 and energetic responses of juvenile Atlantic croaker to salinity. We addressed the following questions:  
72 1) Do juvenile Atlantic croaker display ontogenetic shifts in behavioral salinity preference? 2) Are size-  
73 specific changes in salinity preference consistent with the use of salinity as a migratory cue by which  
74 small juveniles immigrate up estuaries and by which larger individuals emigrate from oligohaline  
75 nurseries? 3) Are energetic processes (feeding rate, growth rate, and gross growth efficiency) affected  
76 by oligohaline versus mesohaline salinity regimes? 4) Do juvenile Atlantic croakers exhibit behavioral  
77 and energetic responses to salinity that provide insights into the potential impacts of climate change on  
78 processes of immigration and the spatial distribution of their estuarine nursery habitat?

## 80 **METHODS**

81 *Fish collection and maintenance* – Postlarval Atlantic croakers (16-18 mm standard length (SL)) were  
82 collected from lower Delaware Bay using an epibenthic sled with 0.5 mm mesh during November and

83 December. Fish were maintained in the laboratory at 18°C and 10‰ under a 12L:12:D photoperiod.  
84 These abiotic conditions corresponded to those commonly experienced by juveniles during fall ingress,  
85 and the following spring, in MAB and northern South-Atlantic Bight (SAB) estuaries (see multi-year  
86 temperature data from the National Data Buoy Center <https://www.ndbc.noaa.gov/>).

87 Trials involving smaller fish were conducted first. As the rest of the fish grew in the holding  
88 tank, trials involving these larger fish were conducted. Trials with the smallest fish began in January and  
89 trials with the largest fish were completed in May.

90 *Behavioral salinity preference* – Behavioral salinity preference experiments were conducted in two 210-  
91 liter modified Staalnd devices (Figure 1). Staalnd devices have been used to examine salinity  
92 preferences in a variety of fishes (Fivizzani and Spieler 1978; Lankford and Targett 1994; He and Xie  
93 2013). Each device consisted of a 122 x 56 x 30.5 cm plexiglass tank partitioned into five compartments  
94 with a series of opaque baffles. The baffles allowed a horizontal salinity gradient to be created across  
95 compartments by resting lower-density (less saline) water above higher-density (more saline) water.  
96 Salinity gradients were created using the modified filling method of Fivizzani and Spieler (1978). Tanks  
97 were filled to a level approximately 10cm above the top edge of the lower baffle (Figure 1), a depth  
98 sufficient to allow fish to swim between compartments (salinities).

99 Two Staalnd devices were used during each trial, during which a gradient tank and a control  
100 tank were run concurrently (Figure 1). A salinity gradient was created in the top device, providing  
101 juveniles with a choice of 2, 6, 10, 14 and 18‰ water. The control device was immediately underneath  
102 and contained 10‰ water in all compartments. Water temperature was maintained at 18±0.5°C during  
103 all trials.

104 Trials were initiated by placing one juvenile Atlantic croaker into the middle compartment  
105 (10‰) of the gradient device and one juvenile into the middle 10‰ compartment of the control device  
106 (Figure 1). The position of individuals in both devices was then recorded at 15 minute intervals for 4  
107 hours. Ten individuals from each of four size classes (26-40, 41-55, 56-70, and 71-85 mm standard  
108 length) were tested. Gradient devices were tested following each trial by sampling the salinity of water  
109 from above and below each discontinuity layer to confirm that salinity gradients had remained intact  
110 throughout the trial. Each device was then drained and reestablished after each trial to eliminate any  
111 residual odors which might influence compartment or salinity preferences.

112 Data from control trials were analyzed to determine whether fish showed inherent preferences  
113 for, or avoidances of particular compartments within the Staaland device that were not related to  
114 salinity. If present, such biases could confound the detection of salinity preferences in the gradient  
115 trials. Using control trial data, Chi-square goodness of fit tests ( $\alpha = .05$ ) were performed for each size  
116 class of fish to test whether the observed frequencies of occurrence of fish in each compartment  
117 differed from the expectation that, in the absence of any inherent biases, frequencies of occurrence  
118 would be equal across compartments.

119 Behavioral salinity preferences were then assessed by comparing the distribution of fish across  
120 salinities in the gradient device to the distribution of fish across compartments in the control device  
121 using contingency table analysis (Legendre and Legendre 1983) where Staaland compartments ( $n = 5$ )  
122 were designated as table rows and Staaland devices ( $n=2$ : gradient versus control) were designated as  
123 columns. Behavioral salinity preference or avoidance was assessed for each salinity offered by first  
124 computing:  $Z_i = |O_i - E_i| / \sqrt{O_i (1 - O_i / N)}$  where  $O_i$  = observed frequency at salinity  $i$ ;  $E_i$  = frequency in  
125 corresponding control compartment  $i$ ; and  $N$  = total number of observations (Legendre and Legendre  
126 1983). The  $Z_i$  values computed for each salinity offered were then compared to the test statistic  $Z_{1-\{\alpha/(2rc)\}}$   
127 where  $Z$  is the abscissa of the standardized normal curve;  $\alpha$  = adopted probability level of 0.05; and  $r$   
128 and  $c$  equal the number of rows and columns in the contingency table, respectively.  $Z_i$  values larger than  
129  $Z_{1-\{\alpha/(2rc)\}}$  indicated that  $O_i$  values were significantly different from  $E_i$  at the probability level of  $\alpha = 0.05$ .  
130 For this test statistic, the denominator term ' $\alpha/(2rc)$ ' was used instead of ' $\alpha/2$ ' in order to account for  
131 the increased probability of observing a value  $|O_i - E_i|$  as large or larger than the one obtained due to  
132 multiple testing of the  $r \times c$  cells of the contingency table simultaneously (Legendre and Legendre 1983).  
133

134 *Energetic response to salinity* – The influence of salinity on the energetics of juvenile *M. undulatus* was  
135 examined by comparing the feeding and growth rates, and growth efficiency, of individuals at 18°C  
136 under oligohaline (2‰) versus mesohaline (18‰) conditions. Two size classes of fish were examined  
137 (30-40 mm and 75-85 mm SL) corresponding to the smallest and largest individuals tested previously for  
138 salinity preferences.

139 Juveniles ( $n=10$  fish per salinity treatment) were held individually in circular 12-liter containers  
140 through which either 2‰ or 18‰ water was recirculated. Fish were acclimated to these salinities at  
141 18°C for 1 week. Each fish was then measured ( $\pm 0.5$  mm SL) and weighed ( $\pm 0.1$ mg). On each of the

142 following 10 days, each fish was provided a pre-weighed, *ad libitum* ration of frozen mysid shrimp  
143 (*Neomysis americana*) and allowed 24 hours to feed. After 24 hours, uneaten mysids were retrieved,  
144 weighed, and replaced with another *ad libitum* ration. Prey not retrieved was assumed to have been  
145 eaten. Fish were re-measured and re-weighed after 10 feeding days for calculation of *ad libitum* feeding  
146 rate, specific growth rate, linear growth rate, and gross growth efficiency (Lankford and Targett 1994).

147 Daily specific feeding rate (FR; % body weight day<sup>-1</sup>) was calculated as:  $FR = C_t W_t^{-1} \times 100\%$ ;  
148 where  $C_t$  = weight of mysids consumed on day t and  $W_t$  = predicted body weight of a fish on day t.  $W_t$   
149 was estimated assuming exponential growth:  $W_t = W_0 e^{Gt}$ ; where  $W_0$  = initial body weight,  $G$  =  
150 instantaneous growth coefficient (see below), and t = time in days (Ricker 1979). Daily specific feeding  
151 rates for each fish were averaged to obtain a mean daily specific feeding rate for each individual. Daily  
152 specific growth rate (SGR; % body weight day<sup>-1</sup>) was calculated for each fish as:  $SGR = (e^G - 1) \times 100\%$ .  $G$   
153 was calculated as:  $[(\ln W_t - \ln W_0) d^{-1}]$ ; where  $W_t$  = body weight after t days,  $W_0$  = initial body weight,  
154 and d = duration of experiment in days. Daily linear growth rate (LGR) was calculated for each fish as:  
155  $LGR = G_L d^{-1}$ ; where  $G_L$  = total linear growth in mm, and d = duration of experiment in days. Gross growth  
156 efficiency ( $K_1$ ) was calculated as  $G I^{-1} \times 100\%$ ; where G = total fish growth (g), and I = total mysid biomass  
157 consumed (g).

158 The effects of salinity on mean FR, SGR, LGR, and  $K_1$  were determined using two-tailed t-tests  
159 ( $\alpha=0.05$ ). SGR and LGR data were logarithmically transformed ( $\log_{10} + 1$ ) prior to statistical analysis to  
160 reduce heteroscedasticity.

161

## 162 RESULTS

163 *Behavioral salinity preference* – During control trials performed without a salinity gradient, juvenile  
164 croaker exhibited equal usage of the five available Staaland device compartments (Table 1). No  
165 significant preference or avoidance of control compartments was detected for any of the four size  
166 classes of fish tested.

167 During trials conducted with a salinity gradient present, small (26-40 mm) juveniles exhibited a  
168 strong preference for higher salinities (14‰ and 18‰) and an avoidance of salinities  $\leq 10‰$  (Figure 2). A  
169 shift toward lower salinities occurred among 41-55 mm juveniles, which only avoided the lowest salinity  
170 (2‰) and this trend continued in 56-70 mm fish, which showed a significant preference for 2‰ and

171 avoidance of 18‰. In contrast to fish in the intermediate size classes, larger (71-85 mm) individuals did  
172 not exhibit statistically significant salinity preference or avoidance (Figure 2). However, we noted that  
173 these larger fish had a tendency to avoid low salinities and prefer high salinities; as frequencies of  
174 occurrence in low salinities ( $\leq 10\text{‰}$ ) were less than expected (based on control results) and frequencies  
175 in 14‰ and 18‰ exceeded expected (Figure 2).

176 *Energetics* - Although mean feeding rate, growth rate, and gross growth efficiency of 30-40 mm juveniles  
177 were all slightly elevated at 2‰ compared to 18‰, the effect of salinity was not statistically significant  
178 (Figure 3). However, there were significant energetic responses of larger juveniles (75-85 mm) to  
179 salinity. Mean specific growth rate and mean linear growth rate of these larger juveniles were >50%  
180 higher at 18‰ than 2‰ (Figure 3). Feeding rate and gross growth efficiency in larger juveniles were  
181 also elevated at 18‰ compared to 2‰ although the differences were not statistically significant (Figure  
182 3).

183

## 184 **DISCUSSION**

185 Previous studies on Atlantic croaker recruitment have indicated that larval ingress into estuaries,  
186 and their up-estuary transport during transformation into juveniles, may be facilitated by both passive  
187 (wind forcing, incoming tidal flows, and residual bottom layer inflow (Hare et al. 2005)) and active  
188 (bottom layer oriented behavior and flood tide transport (FTT; sometimes referred to as selective tidal  
189 stream transport)) processes (Weinstein et al. 1980; Joyeux 1999; Reiss and McConaugha 1999; Hare et  
190 al. 2005; Schaffler et al. 2009; Schieler et al. 2014; Hale and Targett 2018). Furthermore, increased  
191 reliance on active behavioral responses has been reported to occur with ontogenetic development in  
192 young croakers (Hare et al. 2005; Hale and Targett 2018). Our finding that 26-40 mm croakers showed  
193 strong behavioral preferences for high salinities in the laboratory supports that active selection  
194 behaviors continue ontogenetically and assist up-estuary transport of early juveniles in this size range.

195 The general pattern of estuarine circulation consists of residual (net) outward flow of lighter  
196 riverine water at the surface and residual up-estuary flow of heavier oceanic water along the bottom  
197 (Dyer 1997; MacCready and Banas 2011; Valle-Levinson 2011). Attraction of 26-40 mm croakers to  
198 more saline bottom waters, having residual up-estuary flow, and avoidance of less-saline surface waters,  
199 particularly during ebb tide, would promote landward transport of early juveniles to oligohaline nursery  
200 areas. Larger (56-70 mm) juveniles exhibited an ontogenetic shift in salinity preference and preferred

201 lower salinities in our experiments. This shift in preference may play an important role in promoting the  
202 retention of larger juveniles within low salinity habitats where predation risks are presumably lower  
203 (Ross 1983; Day et al. 1989). Interestingly, the preference for lower salinities disappeared in the largest  
204 size class (71-85 mm) of juveniles tested. Moser and Gerry (1989) found that juvenile Atlantic croakers  
205 >70 mm standard length exhibited more rapid metabolic adjustments to salinity increases than those  
206 <70 mm, suggesting that a physiological metamorphosis occurs at this size and may facilitate the  
207 emigration or 'bleeding off' of larger juveniles to more saline habitat described by Yakupzack et al.  
208 (1977). Our finding that 71-85 mm juveniles achieved significantly faster growth rates at 18‰ than 2‰  
209 helps explain reported patterns of down-estuary movement by these larger juveniles.

210 Studies of salinity effects on the energetics of marine and freshwater fishes often reveal lower  
211 metabolic rates and higher somatic growth rates at intermediate salinities (Boeuf and Payan 2001;  
212 Bernatzeder et al. 2010; Thompson 2019). This pattern is commonly attributed to decreased  
213 osmoregulatory costs at intermediate (isosmotic) salinities (Ern et al. 2014). Such costs may provide a  
214 mechanistic link to help understand spatial distribution patterns of fishes in estuaries, as well as findings  
215 that some fishes behaviorally avoid low salinity conditions (Lankford and Targett 1994; Christensen and  
216 Grosell 2018).

217 Interestingly, our laboratory experiments on feeding and growth of small (30-40 mm) juvenile  
218 Atlantic croakers revealed no significant elevation in energetic costs for fish held in oligohaline  
219 conditions relative to mesohaline conditions (at least not at 18°C). This suggests that the immigration to  
220 oligohaline areas by early juvenile Atlantic croakers during spring may be driven by other factors such as  
221 thermal preferences, increased food availability, or reduced predation risks. In fact, Ross (1983)  
222 reported that juvenile Atlantic croakers residing in North Carolina tidal creek nurseries experienced  
223 lower mortality rates in oligohaline areas compared to downstream polyhaline areas, but that growth  
224 rates were similar between areas. It also appears that oligohaline conditions become energetically  
225 advantageous to small juveniles at warmer water temperatures than 18°C tested in the present work.  
226 Peterson et al. (1999) examined salinity effects on growth of small Atlantic croakers (10-20 mm total  
227 length) at warmer (24-27°C) temperatures and found that individuals grew considerably faster at 5‰  
228 than at 20‰. Temperatures in this range occur by early summer (June-July) in estuaries in most of the  
229 MAB, and SAB (see multi-year graphs of mean and median monthly temperatures from the National  
230 Data Buoy Center <https://www.ndbc.noaa.gov/>). Furthermore, shallow oligohaline nurseries generally  
231 warm more quickly in the spring than deeper, more saline habitats (Miller et al. 1985; Lankford and



232 Targett 1994). Therefore, the benefit to small juveniles of immigrating to these areas may be an earlier  
233 start to the growing season. A similar pattern was observed by Lankford and Targett (1994) for juvenile  
234 weakfish (*Cynoscion regalis*), another sciaenid occupying a range of salinities during their nursery  
235 season.

236 Climate change impacts on global temperature, and the level and pattern of regional  
237 precipitation, have ongoing and predicted impacts on estuarine and marine systems (Burrows et al.  
238 2011; Trenberth 2011; Konapala et al. 2020; Colombano et al. 2021). A recent analysis projected that  
239 watersheds of the eastern United States and northern Gulf of Mexico, which already experience  
240 relatively high precipitation on a global comparative basis, will experience higher precipitation,  
241 particularly from May through September (Konapala et al. 2020). Increases in estuarine temperature  
242 and freshwater inflow have relevance for dynamics of the nursery phase of young Atlantic croakers.

243 The dynamics of estuarine circulation is a complex competition among riverine input, tidal flow,  
244 vertical mixing, and bathymetric effects on strength of the residual up-estuary bottom flow (MacCready  
245 and Banas 2011; Valle-Levinson 2011). In coastal plain/drowned river valley estuaries, which are  
246 common in temperate latitudes (Valle-Levinson 2011), increased precipitation and associated increases  
247 in river flow concentrated in the surface water will increase estuarine stratification and can strengthen  
248 residual bottom layer inflow of higher salinity water (MacCready and Geyer 2010; Ross et al. 2021). For  
249 Atlantic croaker, increased river flow, particularly during the fall period of larval ingress and up-estuary  
250 movement of early juveniles, should result in more favorable transport conditions, based on behavioral  
251 attraction of early juveniles to higher salinity, and avoidance of lower salinity, demonstrated by the  
252 present work. Increased river flows may also cause downstream movement of oligohaline nursery  
253 conditions in which Atlantic croakers aggregate as juveniles during spring and summer.

254 Temperature increase causes changes in the phenology (timing of immigration and emigration)  
255 of fishes into and out of estuaries, whereby summer residents generally exhibit earlier ingress and later  
256 egress; a global response pattern across taxa (Langan et al. 2021; Poloczanska et al. 2013). Summer  
257 temperatures exceeding a species' thermal tolerance threshold, however, would likely impact the  
258 phenological response by causing egress to occur earlier (Neuheimer et al. 2011; Thaxton et al. 2020).  
259 Warming will likely cause earlier larval ingress and up-estuary movement by young Atlantic croakers to  
260 oligohaline nursery areas. In fact, on the southeastern United States coast the beginning of larval  
261 ingress of Atlantic croakers and other species is already shifting earlier in warmer years, resulting in

262 longer ingress duration (Thaxton et al. 2020). Projections of future ingress shift, in response to 2°C  
263 warming, are on the order of four weeks for Atlantic croaker. Increased estuarine temperature may also  
264 result in earlier down-estuary emigration of young Atlantic croakers, and perhaps other estuary-  
265 dependent fishes, from oligohaline nurseries to mesohaline and polyhaline areas due to energetic stress  
266 from the interaction of high temperatures and lower salinities, as observed by Lankford and Targett  
267 (1994) for juvenile weakfish.

268 Average temperature during spring, summer, and fall in the Great Bay estuary, New Jersey, in  
269 the central MAB, shows a trend of increasing temperature from about 1980 through 2007 at the end of  
270 the time-series examined (Able and Fahay 2010). During this time, abundance of ingressing larval  
271 Atlantic croakers was particularly evident beginning in the mid-1990s (Hare and Able 2007; Able and  
272 Fahay 2010). It is likely that this increased larval abundance is strongly influenced by more northerly  
273 spawning in the central MAB (Hare and Able 2007; Able and Fahay 2010). Continued warming in the  
274 MAB could extend the northern range of estuarine nursery areas via a combination of northward  
275 progression of spawning, and thus larval ingress, plus more thermally suitable conditions for growth of  
276 young Atlantic croakers in estuaries farther north in the MAB.

277 Further research is warranted on a) behavioral and energetic responses of other estuary-  
278 dependent fishes to estuarine salinity gradients in a warming environment and b) how possible changes  
279 in patterns of movement and estuarine habitat utilization affect processes of recruitment into adult  
280 populations. Temperature and salinity have marked individual and interactive effects on energy  
281 metabolism, and influence growth processes and movement patterns. Temperature increases due to  
282 climate change are likely to have particularly strong effects on fish physiology, fish populations, and  
283 fisheries; and a mechanistic understanding of species' responses is essential to predict the vulnerability  
284 of populations to climate change (Able and Fahay 2010; Little et al. 2020).

285

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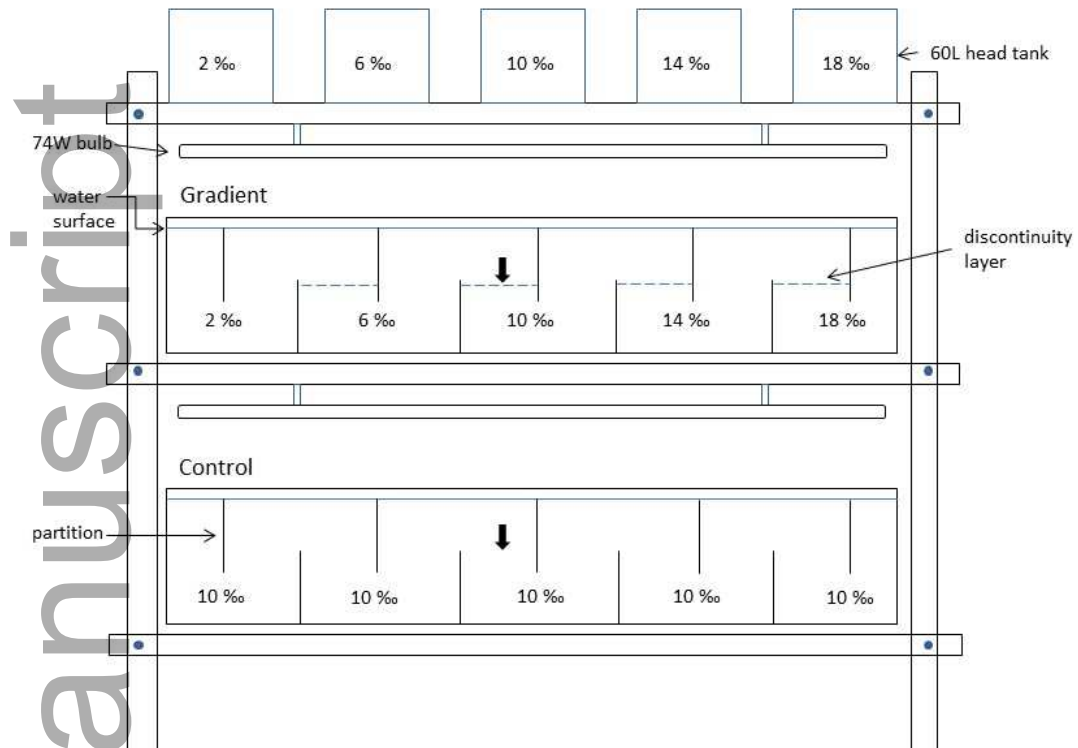
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Table 1. Observed versus expected frequencies of occurrence of juvenile Atlantic croaker size classes for each of the five Staalnd device compartments from control trials. Conditions in each compartment were 10‰ at 18°C. Chi-square ( $X^2$ ), degrees of freedom (df) and probability (p) values represent results of a goodness-of-fit test to evaluate whether each size class of fish showed inherent preference or avoidance of compartments in the absence of a salinity gradient.

Staalnd device compartment	Expected frequency	Observed frequency			
		26-40 mm	41-55 mm	56-70 mm	71-85 mm
1 (left end)	30	35	36	31	26
2	30	31	22	28	37
3 (middle)	30	32	32	30	32
4	30	21	32	29	26
5 (right end)	30	31	28	32	29
	$X^2$	3.733	3.721	0.333	2.87
	df	4	4	4	4
	p	0.44	0.45	0.98	0.58





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452 Figure 1. Diagram of the Staaland devices used to investigate behavioral salinity preference of juvenile  
 453 Atlantic croaker. Arrows indicate the compartments into which a fish was placed at the start of each  
 454 trial.

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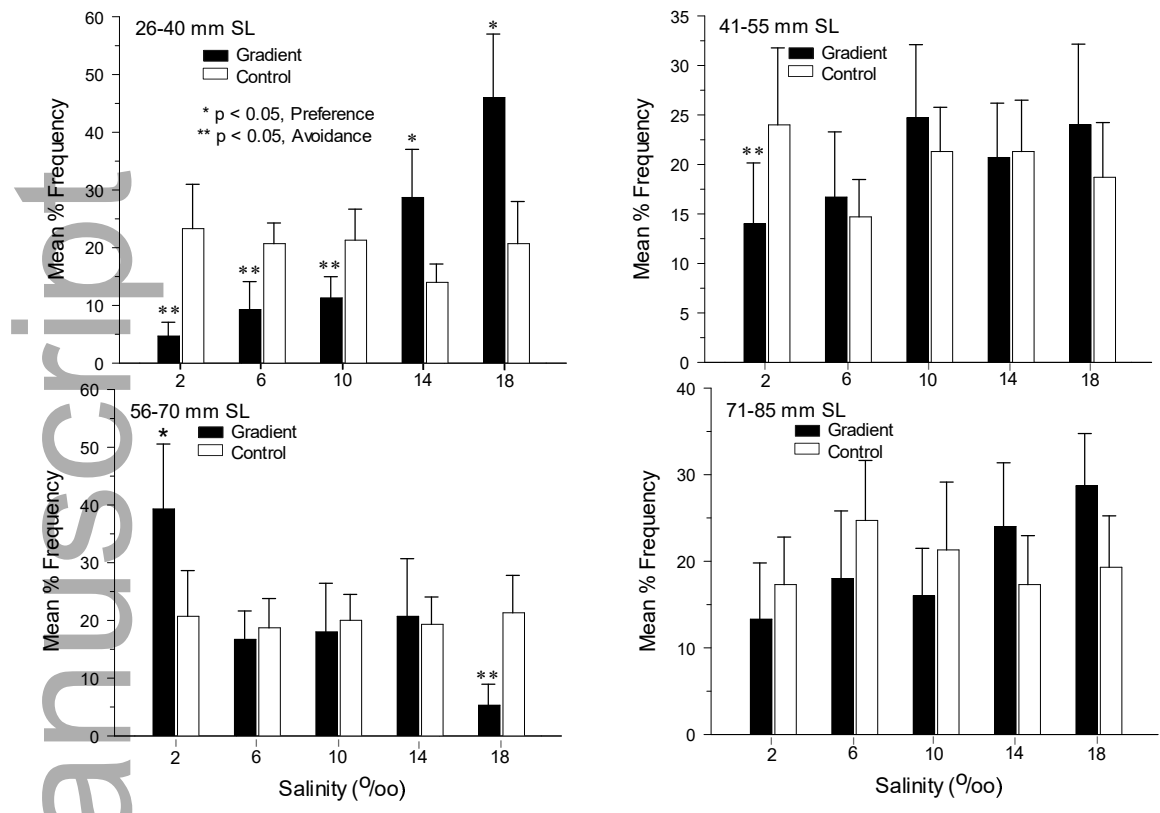
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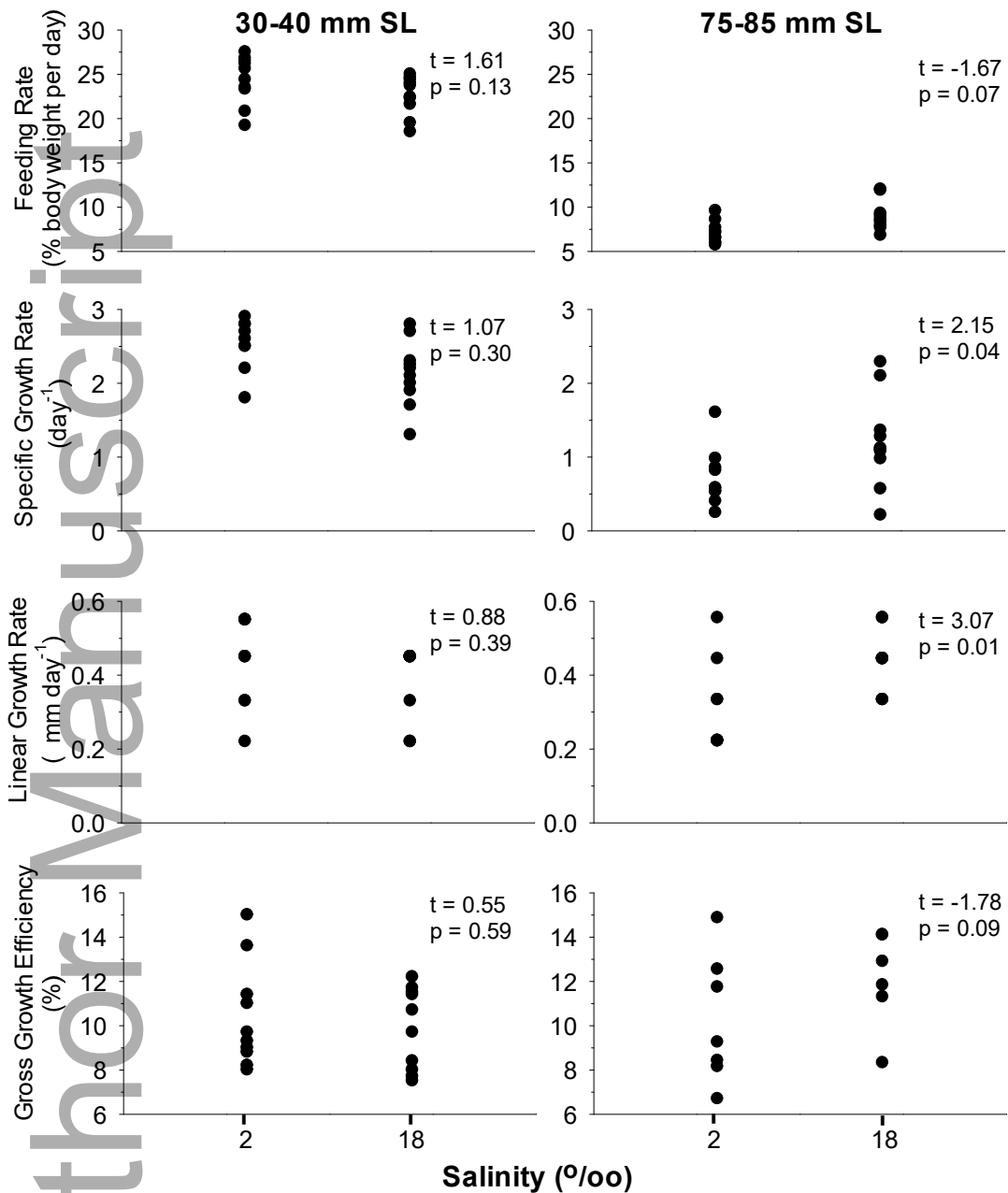
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Figure 2. Behavioral responses of four size classes (SL = standard length) of juvenile Atlantic croaker to a salinity gradient at 18°C. Vertical error bars represent  $\pm 1$  standard error.



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471 Figure 3. Individual feeding rate, specific growth rate, linear growth rate, and gross growth efficiency  
 472 ( $K_1$ ) for two size classes (SL = standard length) of juvenile Atlantic croaker acclimated and tested at 2‰  
 473 versus 18‰ at 18°C (n=10 individual fish per salinity treatment; note that overlap obscures some  
 474 individual data points and gives the appearance of fewer than 10 individual fish per panel, particularly  
 475 for Linear Growth Rate).