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# Vertical distribution of larval Atlantic menhaden (*Brevoortia tyrannus*) and Atlantic croaker (*Micropogonias undulatus*): implications for vertical migratory behavior and transport

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**RUNNING HEAD**:

*Vertical distribution and larval fish transport*

8  **ABSTRACT**

9  Understanding the interaction between biophysical processes is essential to determining how the

10  environment affects transport and survival of fishes. We examined vertical distribution in larval

11  Atlantic menhaden (*Brevoortia tyrannus*) and Atlantic croaker (*Micropogonias undulatus*) using

12  126 depth stratified tows in Delaware Bay, USA, during two cruises, in December 2007 and

13  February 2008. Menhaden larvae were 16.8-24.6 and 20.5-26.2 mm standard length in December

14  and February. Corresponding lengths for croaker were 9.3-17.9 and 8.6-19.6 mm. Using

15  empirical observations, and statistically derived models, we explored larval concentration for

16  both species as a function of location, depth, diel period, tidal period, size, and pair-wise

17  interactions. Menhaden concentration was best modeled as a function of station, cruise, and

18  interactions between depth and size as well as between station and cruise. No significant

19  differences in larval menhaden concentration were present among tidal and diel periods. Croaker

20  concentration was best modeled as a function of size and interactions between station and diel

21  period, depth and size, cruise and size. Despite tidal period not emerging as a significant model

22  parameter, we observed larger croaker larvae during nighttime flood tides. Our statistical models

23  are consistent with processes of up-estuary transport for both species, suggesting larvae are

24  increasingly affected by behavioral responses as larvae grow, exhibiting stronger patterns in

25  vertical distribution. The results refine our understanding of the potential importance of size-

26  related differences in vertical distribution for larval transport in these species. Future research

27  should examine the interactions among size-specific vertical migratory capabilities, vertical

28  distribution, transport, and retention.

29

30  **KEY WORDS**:

31  Distribution, transport, Delaware Bay, croaker, menhaden, larvae, ingress, fish

32  **INTRODUCTION**

33  Vertical distribution impacts survival during the larval stage, and annual recruitment variability,

34  by regulating encounters with prey and predators as well as by influencing the speed and

35    direction of larval transport (Fiksen *et al*., 2007; Miller, 2007; Hurst *et al*., 2009). Larval and

36    juvenile fishes exhibit a range of patterns in vertical distribution in the marine environment,

37    depending upon their behavior and abiotic factors such as hydrodynamics (Heath, 1992, Sabates,

38    2004). Many species exhibit migratory behaviors, which affect transport from spawning grounds

39    to nursery habitats (Kendall and Naplin, 1981; Lyczkowski-Shultz and Steen, 1991; Sabates,

40    2004). However, activity patterns vary across taxa, ontogenetic stages, and along spatial and

41    temporal environmental gradients; all of which affect vertical distribution and horizontal

42    transport (Barnett *et al.,* 1984; Leis, 1991; Heath, 1992; Lough and Potter, 1993; Gray, 1998;

43    Love *et al*., 2009; Lozano and Houde, 2013). Our understanding of vertical migratory behaviors

44    and capabilities in marine fish larvae at the species and ontogenetic stage level, and differences

45    with location, as they relate to transport dynamics is much less extensive than our understanding

46    of the circulation dynamics between estuaries and adjacent coastal areas (Hurst *et al.,* 2009; Leis

47    2010). Determining how marine fish larvae are vertically distributed is critical to understanding

48    transport dynamics into, and within, estuarine nursery areas as well as assessing the impacts of

49    transport on survival.

50        Atlantic menhaden (*Brevoortia tyrannus*; hereafter menhaden) and Atlantic croaker

51    (*Micropogonias undulatus*; hereafter croaker) are of significant commercial interest, occupy

52    important niches in coastal marine food webs, and spawn over a broad geographic range along

53    the continental shelf of the Northwestern Atlantic Ocean (Norcross and Austin, 1986; Barbieri *et*

54    *al.,* 1994; NOAA 2012). Menhaden begin spawning in the early fall and migrate southward as

55    the fall and winter advance (Bourne and Govoni, 1988) with peaks in spawning occurring in fall

56    into early winter in the Middle Atlantic Bight (MAB) (Light and Able, 2003).  Croaker spawn

57    during autumn in the MAB from Cape May, New Jersey, to Cape Hatteras, North Carolina.

58    Concentrations of spawning adults occur on the continental shelf in the southern part of the

59    MAB where water temperatures stay above 16°C (Norcross and Austin, 1988).  Spawning also

60    occurs in estuaries from August-September, however, as autumn progresses spawning adults

61    move into deeper shelf waters seeking preferable water temperatures to spawn (Barbieri *et al*.,

62    1994) and overwinter (Thorrold *et al*., 1997). The appearance of early stage croaker and

63    menhaden in Delaware Bay during winter months is the result of transport by offshore and

64    nearshore currents during this critical period of peak ingress into estuaries along the MAB

65    (Schieler *et al*. 2014).

66    Larval menhaden have been reported to exhibit diel vertical migration affecting potential

67    horizontal transport processes. Govoni and Hoss (2001) found swimbladder development in

68    menhaden occurs 12 days posthatch when larvae are approximately 8 mm in length (notochord),

69    requiring larvae to migrate to surface waters. Forward *et al.,* (1999) reported that intermediate

70    sized larvae (9-27 mm TL) continued diel vertical migration as they developed and ingressed

71    into Beaufort Inlet, North Carolina. However, another study found no diel periodicity in the

72    vertical distribution of menhaden over the continental shelf of North Carolina (Govoni and

73    Pietrafesa, 1994). Similarly, more recent studies have also demonstrated a lack of consistent

74    vertical distribution patterns in menhaden larvae (Lozano and Houde, 2013) suggesting that

75    processes other than vertical migratory behaviors are important to estuarine ingress; processes

76    such as wind driven flux (Hettler and Hare, 1998; Joyeux, 2001; Valle-Levinson *et al*., 2001;

77    Hare *et al*., 2005; Lozano and Houde, 2013; Schieler *et al*. 2014), and residual bottom layer

78    inflow (Weinstein, 1980; Hare *et al*., 2005; Lozano and Houde, 2013).

79    Larval croaker have been reported to occupy distinct depths as a result of ontogenetically

80    changing vertical migratory behaviors. Comyns and Lyczowski-Shultz (2004) found that croaker

81    larvae smaller than 6 mm standard length (SL) showed a distinct pattern of vertical distribution

82    in the Gulf of Mexico. Most larvae (86 %) < 6 mm SL were at the deepest inshore depths (12-16

83    m) during night. Lower concentrations of larger larvae (mean = 6.0 - 6.7 mm SL) occurred in

84    shallower water 1 – 11 m deep, and most were 1 m below the surface during night. Hare *et al*.,

85    (2005) suggested croaker ingress into Chesapeake Bay resulted from behaviorally controlled

86    vertical position co-varying with the tidally dominated flow field and passive up-estuary

87    movement during periods of net up-estuary water flow. In that study, croaker were reported to

88    utilize three mechanisms of ingress including wind forcing, residual bottom layer inflow, and

89    tidal forcing with a steady increase in the use of tidal forcing (selective tidal stream transport) as

90    larval development proceeded (Hare *et al.* 2005).

91    Despite a growing body of knowledge concerning biophysical processes affecting larval

92    fish ingress (e.g. Churchill *et al.* 1999; Jager and Mulder 1999; Joyeux, 1999; Rowe and

93    Epifanio, 1999; Hare *et al*., 2005; Schieler *et al*. 2014; Teodósio *et al.,* 2016), an understanding

94    of the interaction between physical and biological factors impacting transport remains poorly

95    understood (Teodósio *et al.,* 2016). Indeed, mechanisms impacting transport require critical

96    evaluation (Lozano and Houde, 2013) to determine how these processes affect delivery into

97  estuarine nursery areas for these species through a range of sizes and potential behavioral

98  capabilities. Previous studies have used the flux of larvae resulting from wind forcing, residual

99  bottom layer inflow and tidal forcing (e.g. Hare *et al.* 2005) or correlations with episodic

100 environmental phenomena (e.g. Schieler *et al.* 2014) to suggest potential modes of ingress.

101 However, no previous studies have developed empirically derived, species-specific, generalized

102 linear models of ingress. Developing statistically-based models of larval concentration based on

103 *in situ* collections would help us understand how processes affecting transport may be acting on

104 aggregations of larval fish, thereby providing opportunities to explicitly examine previously

105 suggested modes of ingress.

106       This study was designed to examine the vertical distribution of larval menhaden and

107 croaker at the mouth of Delaware Bay during late fall and winter (2007-2008) to assess vertical

108 distribution and potential species-specific transport mechanisms. Our primary objective was to

109 derive species-specific, statistically based, generalized linear models of concentration as a

110 function of physical parameters and larval size, as well as pair-wise interactions among those

111 parameters collected *in situ*, to model larval menhaden and croaker concentration. Specifically,

112 we examined how concentration varied as a function of cruise, station, depth within the water

113 column, diel period, tidal period, mean length and all two-way interactions among those factors.

114 Our secondary objective was to use the derived models to better understand processes affecting

115 larval transport in these species, consider how the parameters that significantly affected observed

116 concentration provide support for several potential modes of ingress, and propose specific areas

117 for future research.

118

119 **METHODS**

120 *Study site*

121 Delaware Bay is a weakly stratified coastal plain estuary that extends >200 km from Trenton, NJ

122 down to the mouth at Cape May, NJ. The bay has a single channel, 45 m in depth that runs along

123 the longitudinal axis and extends onto the continental shelf (Janzen and Wong, 2002).

124 Circulation into the estuary is variably dominated by wind and buoyancy with typical two-layer

125 estuarine circulation occurring in the absence of strong wind events that vertically mix the water

126 column (Epifanio and Garvine, 2001). Winds shift seasonally in direction from south to north

127 during the fall, and freshwater input generally declines, creating periods of mixed conditions

128 varying in intensity in the bay.  North-northeasterly alongshore wind events can enhance across

129 shelf flow through Ekman transport (Epifanio and Garvine, 2001, Whitney and Garvine, 2005)

130 and along-estuary (northwesterly) wind events can drive periods of enhanced up-estuary bottom

131 layer flow by creating internal slopes in the bay (Janzen and Wong, 2002, Wong and Vale-

132 Levinson, 2002).

133 *Field and laboratory methods*

134 Sampling was conducted at the mouth of Delaware Bay during two cruises on the R/V Hugh R.

135 Sharp, 6-7 December 2007 and 28-29 February 2008 at five stations across the bay mouth and

136 six nearshore stations (Fig. 1). A CTD (conductivity-temperature-depth) profile was conducted

137 just prior to ichthyoplankton collection at each station. For each sample, tow depth was assigned

138 as bottom=1 and surface=2; diel period as dawn=1, day=2, dusk=3, and night=4 with periods of

139 civil twilight used to characterize dusk and dawn (USNO, 2012); tidal period  as ebb =1, slack

140 =2 (prior to ebb/flood) and flood =3 using predicted current data (NOBELTEC). Mean

141 temperature, salinity and density were calculated for surface and bottom samples after depth was

142 converted from pressure (UNESCO, 1983). Mean wind stress over each day for each cruise was

143 calculated using data from NOAA weather station LWSD1 (Fig. 1).

144 Ichthyoplankton samples were collected using a 1 m$^2$ Tucker trawl with 1 mm mesh.

145 Separate 4 minute oblique, surface (midpoint to surface) and bottom (bottom to midpoint) tows

146 were taken at each station above and below the midpoint of the water column if no pycnocline

147 was detected or above and below the pycnocline if one was detected. Each station was sampled,

148 on average, 2.5 times (+/- 0.13 SEM) during the December cruise and 3.3 times (+/- 0.24 SEM)

149 during the February cruise. A total of 27 bottom and surface samples were collected during the

150 first cruise and 36 during the second cruise (126 depth-discriminate samples in total). Samples

151 were washed from the net, sieved (1 mm mesh), and preserved in 95% ethanol. In the laboratory,

152 the number of menhaden and croaker, and mean length of a random subsample of 20 individuals

153 of each species, were recorded for each sample. Volume of water filtered was calculated using

154 flow meter data (General Oceanics Model 2030, standard rotor, Miami, FL). Larval

155 concentration was calculated as individuals per 1000 m$^3$.

156 *Statistical analyses*

157 Larval menhaden and croaker concentration data were fourth root transformed prior to all

158 analyses, to approximate a normal distribution among station and depth strata. An automated

159  approach using the 'glmulti' package (Calcagno 2013) with generalized linear models and the

160  'glm' function (R Development Core Team 2010) was applied to statistically model larval

161  concentration as a function of significant main effects and pairwise interactions among cruise,

162  station, depth, diel period, tidal period and mean length (Calcagno and de Mazancourt 2010).

163  Mean length was considered a quantitative covariate while the remaining five explanatory

164  variables were considered categorical. All candidate models were considered for each species (n

165  = 514,800) and ranked according to information criterion. The most parsimonious model for

166  each species was selected using the small-sample size corrected Akaike Information Criteria

167  (AICc) and considered to best represent larval concentration after an exhaustive screening

168  process (Calcagno and de Mazancourt 2010). Paired-sample t-tests were used to examine

169  differences in mean larval length for each species between surface and bottom, as well as mean

170  water temperature, salinity, and density between surface and bottom tows for each cruise using

171  SYSTAT Version 13.0. Inference for all statistical analyses was made at $\alpha = 0.05$.

172

173  **RESULTS**

174  Physical conditions differed by depth and between cruises. Mean temperature ($p < 0.001$) and

175  density ($p = 0.002$) varied significantly by depth during the December cruise, with lower

176  temperatures and densities in surface waters (Table 1); but salinity did not differ significantly by

177  depth ($p = 0.733$). During the February cruise however, temperature, salinity, and density all

178  differed significantly by depth (all p-values $< 0.001$) with higher mean values in bottom waters

179  (Table 1). Winds were predominately out of the north for the duration of the first cruise,

180  primarily north-northeast on 6 December and north-northwest on 7 December; whereas winds

181  were variable during the second cruise, with northwest winds on 28 February and southeast

182  winds on 29 February (Table 2).

183      Four factors were found to best model the concentration of larval menhaden. Based on

184  the corrected AIC (AICc = 447.16) and reduction in residual deviance of the model fit (280.66,

185  112 DF) relative to the null deviance of the intercept (330.50 on 116 DF), the best model to

186  explain transformed menhaden concentration was:

187  Concentration ~ Cruise + Station + Depth*Size + Cruise*Station; where * indicates interaction.

188  Based on visual inspection, residuals of the model were normally distributed compared to the

189  predicted values, while the standard deviance of the residuals suggested that the predicted model

190  fit the data well. Station ($p = 0.438$), and the interaction between Depth and Size ($p = 0.260$) as

191  well as the interaction between Cruise and Station ($p = 0.060$) were not significant main effects

192  despite representing significant parameters in the final model. However, Cruise ($p < 0.001$) was a

193  significant main effect in the generalized linear model. Menhaden concentration varied

194  significantly between the two cruises ($p < 0.001$) with a greater transformed mean concentration

195  observed during the second cruise (3.62 individuals per 1000 $m^3$) compared to the first cruise

196  (2.18 individuals per 1000 $m^3$). Concentration did vary among stations with the highest mean

197  concentration observed at Station 1 (4.57 individuals per 1000 $m^3$), followed by Station 6 (3.81

198  individuals per 1000 $m^3$) and Station 5 (3.68 individuals per 1000 $m^3$). Mean concentration did

199  not substantially vary by depth, diel period, tidal period or size (Fig. 2).

200      No significant differences were detected in mean length of menhaden between depth

201  strata during the first ($p = 0.479$) or second cruise ($p = 0.684$). However, slightly larger

202  individuals were generally observed in surface waters (23.5 mm SL +/- 0.19 SEM) during both

203  cruises compared to bottom waters (23.2 mm SL +/- 0.20 SEM; Fig. 3). The range of mean

204  menhaden size by station during the December cruise was 16.8 - 24.3 mm SL in bottom waters

205  and 18.3 - 24.6 mm SL in surface waters. During the February cruise, mean menhaden size was

206  22.1 - 25.6 mm SL in bottom waters and 20.5 - 26.2 mm SL in surface waters.

207      Four factors were also found to best model the transformed concentration of larval

208  croaker. Based on the corrected AIC (AICc = 340.73) and reduction in residual deviance of the

209  model fit (155.33 95 DF) relative to the null deviance of the intercept (222.20 on 99 DF), the

210  best model to explain croaker concentration was:

211  Concentration ~ Size + Station*Diel Period + Depth*Size + Cruise*Size; where * indicates

212  interaction. Based on visual inspection, the standard deviance of the residuals suggested that the

213  predicted model fit the data well, while the residuals of the model were normally distributed

214  compared to the predicted values. All of the model parameters were found to act as significant

215  main effects within the generalized linear model including Size ($p < 0.001$), the interaction

216  between Station and Diel Period ($p = 0.015$), the interaction between Depth and Size ($p = 0.030$),

217  and the interaction between Cruise and Size ($p = 0.001$). Greater concentrations were typically

218  observed with larger sizes. Greater mean concentration (3.19 individuals per 1000 $m^3$) was

219  observed in the first cruise relative to the second cruise (1.81 individuals per 1000 $m^3$), and in

220  bottom waters (2.69 individuals per 1000 $m^3$) compared to surface waters (2.11 individuals per

221 1000 m$^3$) during both cruises (Fig. 4). Higher mean concentration was observed during dawn and

222 night (2.51 individuals per 1000 m$^3$), compared to day and dusk (2.27 individuals per 1000 m$^3$).

223 The highest mean concentration of croaker was observed at Stations 6 (3.36 individuals per 1000

224 m$^3$), followed by Station 1 (3.35 individuals per 1000 m$^3$) and Station 5 (2.87 individuals per

225 1000 m$^3$). Mean concentration by tidal stage did not vary greatly between flood (2.40 individuals

226 per 1000 m$^3$) and ebb tides (2.43 individuals per 1000 m$^3$); however, both were greater than the

227 mean concentration observed during slack tide (1.89 individuals per 1000 m$^3$; Fig. 4). Further,

228 slightly larger croaker were present during flood tides (12.7 mm SL +/- 0.33 SEM), compared to

229 ebb (12.3 mm SL +/- 0.32 SEM) and slack tides (10.1 mm SL +/- 0.30 SEM).

230 Size of croaker differed significantly between depth strata ($p = 0.007$) during the first

231 cruise, whereas there was no significant difference between depth strata ($p = 0.260$) during the

232 second cruise (Fig. 5). The range of mean croaker lengths by station during the December cruise

233 was 10.1 - 17.9 mm SL in bottom waters and 9.3 - 16.4 mm SL in surface waters. During the

234 February cruise, mean croaker length ranged from 9.4 - 17.7 mm SL in bottom waters and 8.6 -

235 19.6 mm SL in surface waters.

236

237 **DISCUSSION**

238 We developed empirically derived generalized linear models of larval concentration in response

239 to a suite of interacting environmental parameters for both menhaden and croaker. Such models

240 have not been previously available for larval menhaden and croaker. Based on these results, we

241 can refine our understanding of potential transport processes for both species that include

242 statistically significant main effects and pair-wise interactions. We suggest menhaden and

243 croaker larvae display an increasing trend in the use of, or proficiency in, active vertical

244 migratory behaviors with an increase in size, over the range of 16.8 to 26.2 mm SL in menhaden

245 and 8.6 to 19.6 mm SL in croaker. Further, we found evidence to suggest that larger menhaden

246 concentrated in surface waters, despite being disrupted by seasonal mixing; whereas larger

247 croaker were more frequently associated with bottom waters.

248 For menhaden we found concentration varied as a function of cruise and station, as well

249 as an interaction between those parameters. Our results suggest that larval menhaden stratify by

250 size with larger individuals more frequently occurring in surface waters. However, larvae may

251 become mixed throughout the water column, potentially relying on up-estuary transport by

252 physical forcing mechanisms, including tidal, buoyancy and wind driven processes as a principal

253 means of ingress. Similarly, based on modeled results of concentration, we found that croaker

254 larvae rely on periods of net up-estuary water movement created by physical forcing

255 mechanisms. However, unlike menhaden, size alone and an interaction between station and diel

256 period were also found to significantly affect modeled croaker concentration. These results

257 suggest that larger larval croaker, approximately greater than or equal to 12.7 mm SL, become

258 more reliant on active behavioral responses to the environment than larval menhaden ranging in

259 size from 16.8-26.2 mm SL. Specifically larval croaker appear to advance toward nocturnal flood

260 tide transport as a means of ingress as they grow.

261     While our analysis describes how the physical environment and larval size affected

262 concentration of larval menhaden and croaker at depth, as well as refine our understanding of

263 potential transport mechanisms, it was constrained by several factors. Sampling was over two

264 ~50 hour cruises focused on the Delaware Bay mouth; we did not sample further offshore to

265 measure hydrodynamic mixing and subsequent vertical distribution of larval menhaden or

266 croaker, as has been done by others (e.g. Hare and Govoni, 2005). Offshore samples would have

267 been helpful in addressing the issue of selective transport under stratified conditions and

268 variability in transport processes with onshore migration. Although we took oblique tows over

269 the top and bottom half of the water column, discrete depths could not be compared; so our

270 interpretations of larval stratification were somewhat constrained because of a lack of high

271 vertical resolution. Finally, statistically assessing vertical distributions of planktonic larvae is

272 challenging and may not describe the full range of conditions and behaviors fish utilize to ingress

273 into estuaries from coastal oceans (Pearre, 1979). Despite this, our field-based, species-specific

274 models provide new insights into the dynamics of larval ingress into large, coastal plain estuaries

275 by these two ecologically and economically important species.

276     Based on the concertation of larvae at depth we identified key processes impacting larval

277 transport into the estuary. We documented three main factors that affected larval concentration

278 shared by both species including spatial and temporal variability, as well as the size of larvae.

279 Spatiotemporal variability in larval supply was likely generated by patterns in adult spawning

280 and variability associated with net transport from offshore spawning grounds (Quinlan *et al.*

281 1999) as well as from seasonal mixing of waters at the bay mouth (Epifanio and Garvine, 2001).

282 Additionally, our results demonstrate that both menhaden and croaker larvae have an increasing

283  capability to stratify by depth with an increase in size. The interactive effect of depth and size in

284  larvae ranging from 16.8 to 26.2 mm SL in menhaden and from 8.6 to 19.6 mm SL in croaker

285  suggests that as ontogenetic development proceeds and swimming efficiency increases, so too

286  does the efficacy of vertical migratory behaviors (Hare *et al.* 2005; Teodósio *et al.* 2016).

287      We suggest that the interaction among wind driven surface currents, buoyant freshwater

288  discharge, and strong tidal forcing disrupted vertical migratory behavior in menhaden larvae,

289  particularly for smaller individuals, such that there was no observable depth stratification by diel

290  period across sizes. Similar studies for early life stages of species in other taxa (e.g. blue crab,

291  *Callinectes sapidus*) have documented a diel pattern in activity suggesting transport is reliant on

292  wind forcing and density driven flows into Delaware Bay (Biermann *et al.* 2016). Previous

293  studies on menhaden suggest larvae engage in diel migratory behavior (e.g. Hoss *et al.*, 1989;

294  Forward *et al.,* 1996, 1999). However, others have demonstrated a lack of diel periodicity

295  including Govoni and Pietrafesa (1994) in Onslow Bay, NC and a similarly designed study to the

296  present work by Lozano and Houde (2013) in Chesapeake Bay. Given our results and the season

297  of ingress, we suggest surface oriented vertical migratory behaviors are likely being disrupted by

298  strong vertical mixing in surface waters. In the fall and winter when larval menhaden are

299  ingressing into estuaries along the MAB, winds shift, and blow from the northeast, consequently

300  driving periods of intense down-welling circulation with across-shelf Ekman transport creating

301  pulses of subtidal flow into estuaries (Goodrich *et al.,* 1989, Garvine, 1991, Epifanio and

302  Garvine, 2001). Likewise, gravitational circulation driven by buoyant freshwater outflow

303  enhances across-shelf flows, similar to down-welling, near the mouths of large estuaries (Pape

304  and Garvine, 1982, Bourne and Govoni, 1988, Epifanio and Garvine, 2001) creating periods of

305  favorable up-estuary larval transport. In addition, strong tidal currents induce mixing of early life

306  stage fishes in the water column through advection and create transport mechanisms into

307  estuaries during flooding tides (Okubo, 1973, Onishi, 1986, Zimmerman, 1986, Wolanski, 1986,

308  Wolanski *et al.,* 1988, Chant *et al.,* 2000). If menhaden larvae are behaviorally orienting toward

309  the surface as suggested by Forward *et al.* (1996, 1999), and by the interaction between depth

310  and size observed in our study, they would likely become mixed and thus transported within the

311  water in which they are entrained, successfully ingressing during periods of net up-estuary flow

312  and experiencing advection during down-estuary flow.

313    We propose that behavioral processes, whose efficacy is a function of larval size, and
314    physical transport processes are equally important to the estuarine ingress of croaker, with a
315    greater reliance on active behavioral strategies at larger sizes. Croaker, like menhaden rely upon
316    periods of net up-estuary water movement caused by wind, density and tidally driven flows to
317    ingress into estuaries. However, we observed higher concentrations of croaker larvae at larger
318    average sizes, during evening hours and on flood tides.  These results suggest that as croaker
319    larvae develop, there is an increase in active behavioral processes, specifically moving towards
320    nocturnal flood tide transport as the principal mechanism of ingress into estuaries. Similarly,
321    Hare *et al.* (2005) suggested croaker used wind forcing, residual bottom layer inflow and tidal
322    forcing to ingress into Chesapeake Bay, with an increasing reliance on tidal flux for larger sizes.
323    Further, Schieler *et al.* (2014) suggested larval croaker use vertical migrations for up-estuary
324    transport and estuarine retention in Delaware Bay based on correlations between nightly
325    concentrations and time-lagged wind events. Neither Hare *et al.* (2005) nor Schieler *et al.* (2014)
326    examined diel periodicity to compare with our study. However, the work of Schaffler *et al.*
327    (2009) did find larval croaker were more abundant at the mouth of Chesapeake Bay during
328    nighttime collections suggesting the possibilities of net avoidance, or diurnal vertical migration
329    as suggested by previous studies (Raynie and Shaw 1994; Joyeux 1998; Forward and Tankersley
330    2001). Additionally, diel patterns in vertical distribution have been reported for croaker larvae in
331    the Gulf of Mexico, with higher concentrations and greater sizes observed at shallower depths
332    during night collections (Comyns and Lyczowski-Shultz, 2004), suggesting an ontogenetic
333    transition in behavioral capability comparable to that hypothesized by Teodósio *et al.* (2016) and
334    observed in this study.
335    In addition to identifying potential transport processes for larval menhaden and croaker,
336    we compared trends in ingress and size of larvae in our work to those reported previously for
337    these species in the central MAB. The occurrence of menhaden and croaker larvae during both
338    cruises in the current study confirms that both species belong to the winter seasonal group
339    occurring from October and April in Delaware Bay, as described by Ribeiro *et al.* (2015). Larval
340    menhaden have been reported to be abundant on the inshore region of the continental shelf of the
341    MAB from September-November and are common from December-March (Able and Fahay,
342    2010). Larval menhaden ingressing into Delaware Bay estuaries have historically peaked from
343    December through May ranging in size from 10 – 20 mm TL (Wang and Kernehan, 1979); while

344    a more recent study found mean length ranged from 21.6 – 27.1 mm SL (Schieler *et al.* 2014)

345    from mid-November to mid-December. We found that menhaden were more abundant in late

346    February than in early December, as was described by Wang and Kernehan (1979), and more

347    similar in size to the size range reported by Schieler *et al.* (2014). Larval croaker have been

348    collected at Little Sheepshead Creek, New Jersey from August to January with peak ingress

349    occurring from September to November in recent years (Able and Fahay, 2010). Similarly,

350    Miller *et al.* (2003) found larval croaker ingress to occur as early as August in Delaware Bay

351    ranging in size from 2-28 mm TL. While Schieler *et al.* (2014) found nightly mean length of

352    croaker ranged from 12.8 – 17.6 mm SL. Croaker were more abundant in December than

353    February in our study, at a size range similar to those reported by Miller *et al.* (2003), with a

354    mean length similar to what was reported by Schieler *et al.* (2014) during the first cruise (13.0

355    mm SL +/- 0.32). However, mean length during the second cruise (11.8 mm SL +/- 0.30 SEM)

356    was slightly less than the range of nightly mean lengths observed by Schieler *et al.* (2014).

357         Our analysis provides a new assessment of how physical and biological processes

358    potentially interact to impact estuarine ingress of larval menhaden and croaker. Our results

359    suggest that behavioral responses occur within nested environmental, species, and size-specific

360    levels to affect concentration, vertical distribution, and transport. Species- and size-specific

361    differences in vertical distribution indicate how transport is dependent upon the interaction

362    between environmental conditions and behavioral responses. Specifically, we found that the use

363    of behavioral mechanisms affecting up-estuary movements becomes increasingly more important

364    as larvae grow over sizes ranging from 16.8 to 26.2 mm SL in menhaden and from 8.6 to 19.6

365    mm SL in croaker. Our work provides a perspective for considering transport processes in a

366    quantitative framework by developing statistically significant methods for modeling larval

367    concentration. Future research on these species should be directed at exploring the size-specific

368    behavioral responses to environmental variables, suggested here, in greater detail through field-

369    based observations. Incorporation of these interactions into models of larval abundance such as

370    developed here would further advance our understanding of larval menhaden and croaker

371    transport into estuaries and their retention therein.

372    **ACKNOWLEDGEMENTS**

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**Table 1**. Mean temperature, salinity, and density for surface and bottom water during December 2007 (Cruise 1) and February 2008 (Cruise 2). Means with an asterisk indicate a significant (α = 0.05) pairwise difference between surface and bottom values within each cruise.

| Cruise | Parameter | Surface | | | Bottom | | |
|---|---|---|---|---|---|---|---|
| | | Temperature (°C) | Salinity | Density (kg per m-3) | Temperature (°C) | Salinity | Density (kg per m-3) |
| Cruise 1 | Average | 6.54* | 28.56 | 1022.39* | 7.03* | 28.76 | 1023.08* |
| Cruise 1 | Stdev | 1.02 | 1.04 | 0.86 | 1.21 | 3.40 | 0.30 |
| Cruise 1 | SEM | 0.21 | 0.21 | 0.18 | 0.25 | 0.71 | 0.06 |
| | | | | | | | |
| Cruise 2 | Average | 3.92* | 24.65* | 1019.58* | 4.53* | 27.04* | 1021.48* |
| Cruise 2 | Stdev | 0.45 | 2.44 | 1.93 | 0.59 | 1.97 | 1.54 |
| Cruise 2 | SEM | 0.07 | 0.39 | 0.31 | 0.09 | 0.32 | 0.25 |

**Table 2**. Mean east and north components of wind stress (dyn) from NOAA weather station LWSD1 at Lewes, DE during the December 2007 and February 2008 cruises. Means were calculated for each day. The oceanographic convention is used whereby negative north is toward the south and negative east is toward the west.

| | East | North | General wind field |
|---|---|---|---|
| Cruise 1 | | | |
| 12/6/2007 | -1.130 | -3.468 | NNE |

| | | | |
|---|---|---|---|
| 12/7/2007 | 1.401 | -3.209 | NNW |
| Cruise 2 | | | |
| 2/28/2008 | 7.010 | -5.750 | NW |
| 2/29/2009 | -0.998 | 1.576 | SE |

**Figure Legends**

Figure 1. Study area in lower Delaware Bay, with an inset of the Middle Atlantic Bight. Individual ichthyoplankton sampling stations are marked with a black circle and NOAA weather station LWSD1 is shown with a blue circle.
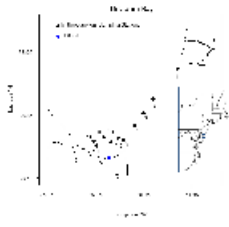
Figure 2. Concentration (4th Root Transformed) of Atlantic menhaden (black dots) with the optimal generalized linear model of concentration (red line), and the standard errors of the fitted model (dashed blue lines).

Figure 3. Standard length (mm) of Atlantic menhaden by cruise and depth at the mouth of Delaware Bay. Cruise 1 occurred in December 2007 and Cruise 2 in February 2008.

Figure 4. Concentration (4th Root Transformed) of Atlantic croaker (black dots) with the optimal generalized linear model of concentration (red line), and the standard errors of the fitted model (dashed blue lines).
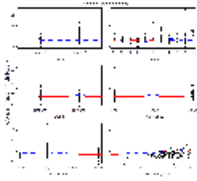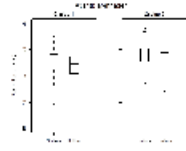
Figure 5. Standard length (mm) of Atlantic croaker by cruise and depth at the mouth of Delaware Bay. Cruise 1 occurred in December 2007 and Cruise 2 in February 2008.

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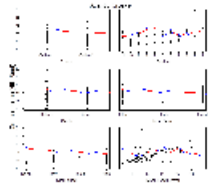
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