Modeling larval fish behavior: Scaling the sublethal effects of methylmercury to population-relevant endpoints

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Abstract

Expressing the sublethal effects of contaminants measured on individual fish as cohort and population responses would greatly help in their interpretation. Our approach combines laboratory studies with coupled statistical and individual-based models to simulate the effects of methylmercury (MeHg) on Atlantic croaker larval survival and growth. We used results of video-taped laboratory experiments on the effects of MeHg on larval behavioral responses to artificial predatory stimuli. Laboratory results were analyzed with a regression tree to obtain the probability of control and MeHg-exposed larvae escaping a real predatory fish attack. Measured changes in swimming speeds and regression tree-predicted escape abilities induced by MeHg exposure were then inputted into an individual-based larval fish cohort model. The individual-based model predicted larval-stage growth and survival under baseline (control) conditions, and low- and high-dose MeHg exposure under two alternative predator composition scenarios (medusa-dominated and predatory fish-dominated). Under MeHg exposure, stage survival was 7–19% of baseline (control) survival, and the roughly 33-day stage duration was extended by about 1–4 days. MeHg effects on larval growth dominated the response under the medusa-dominated predator composition, while predation played a more important role under the fish-dominated predator composition. Simulation results suggest that MeHg exposures near extreme maximum values observed in field studies can have a significant impact on larval cohort dynamics, and that the characteristics of the predator–prey interactions can greatly influence the underlying causes of the predicted responses.

Keywords: Methylmercury; Predator–prey interactions; Individual-based model; Regression tree; Larval fish; Behavior; Population-level effects

1. Introduction

The past few decades of toxicological research have demonstrated that it is difficult to establish a link between sublethal effects of contaminants measured on individuals and indices of population health (Mills and Chichester, 2005). Yet, endocrine disruptors, which interrupt normal signaling processes within and between organisms, generally manifest themselves as subtle changes in the reproductive system, molecular biology, physiology, metabolism, homeostasis, and behavior of an organism (Damstra et al., 2002). Despite intensive study on how endocrine disruptors operate mechanistically (Rotchell and Ostrander, 2003), it often remains unclear as to how the subtle changes caused by endocrine disruptors affect an individual’s performance in a natural setting, or how these changes relate to population-level responses. Ecological death is the phenomenon where animals are not overtly harmed by a contaminant, but exposure causes alterations in their behavior or physiology such that the organism is unable to function ecologically as expected (Mesa et al., 1994; Scott and Sloman, 2004).

Behavior is often used as an endpoint in toxicological studies because an animal’s behavior represents an integrated expression of its physiological response to its environment (Clotfelter et al., 2004). Usually, toxicological studies that monitor behavior include behaviors that show disruption of certain physiological mechanisms. For example, in striped mullet (Mugil cephalus), methylmercury (MeHg) was shown to decrease levels of serotonin, which were then associated with the progressive loss of motor control (Thomas et al., 1981). Increasingly, toxicologi-
Individual-based models (IBMs) are well suited to link laboratory behavioral results to population-relevant indices (Rose et al., 1999, 2003). Individual-based models track each individual; the sum over all individuals at any given time is the cohort or the population. Laboratory toxicological effects that are reported for the individual can be easily imposed on processes represented in an individual-based model, either directly or first via some conversion from a statistical model. If the IBM simulates the appropriate processes, sublethal effects, such as changes in behavior, can be imposed on individuals and the IBM used to predict the population-level response.

In this paper, we used an IBM to scale the laboratory-measured effects of maternally transferred MeHg on larval Atlantic croaker (Micropogonias undulatus) behavior to larval-stage survival and duration. MeHg has been shown to reduce serotonin levels in the brain of fish, inhibit normal development of the hypothalamic serotonergic system (Tsai et al., 1995), and to affect locomotor activity and impair prey capture abilities (Smith and Weis, 1997). In this analysis, we use the experimental results of Alvarez et al. (2006), who documented MeHg effects on the locomotor activity and predator-evasion skills of larval croaker. Expressing these behavioral effects as changes in stage duration and survival helps to place these sublethal effects into an ecological context. Stage duration and survival are fundamental parameters in life tables and matrix projection models of population dynamics. We simulate the effects of a low and high dose of MeHg on larval-stage survival and duration under two alternative predator compositions, and perform simulations to separate the effects of MeHg exposure on larval encounters with their zooplankton prey (growth only) versus MeHg effects on larval encounters with their predators (mortality only). This paper provides methodological details and additional simulation results (two predator compositions; growth versus mortality effects) to the much streamlined and subset of results presented by Alvarez et al. (2006). We conclude with discussion of the usefulness of our approach for relating sublethal effects of contaminants to ecological endpoints, the realism of the modeling results presented, and their possible relevance to field conditions.

2. Methods

2.1. Atlantic croaker as the test organism

The ocean larval stage of Atlantic croaker is a good model organism on which to base the larval fish IBM and to simulate behavioral effects associated with contaminant exposure. Atlantic croaker spawn offshore, and the egg, yolk-sac larval, and early planktonic feeding larval stages experience high mortality rates while in the ocean on their way to their juvenile nursery grounds in estuaries (Diamond et al., 1999). Early life stages that exhibit high and variable mortality rates can be important regulators of year class strength and recruitment dynamics in fish (Houde, 1989; Leggett and Deblois, 1994). The ocean larval stage of croaker may be especially sensitive to behavioral effects because early ocean larvae have to undergo sufficient physiological and behavioral development to exhibit successful foraging (exogenous feeding) and predator evasion. Laboratory experiments have demonstrated how contaminants affect the foraging and predator-evasion behaviors of Atlantic croaker larvae (Faulk et al., 1999; McCarthy et al., 2003; Alvarez et al., 2006).

2.2. Laboratory studies

We used the results of a laboratory study of the effects of MeHg on larval croaker swimming speed and predator-evasion skills (see Alvarez et al., 2006). Briefly, uncontaminated and contaminated food was fed to adult female croaker, who were then spawned and their eggs were collected and analyzed for MeHg. Eggs from individual adults were grouped together based on the MeHg concentrations measured in their eggs: control (<0.05 µg g⁻¹ egg), low-dose exposure (0.01–3.5 µg g⁻¹), and high-dose exposure (>3.5 µg g⁻¹). Eggs from the control, low, and high MeHg dose treatments were then hatched in the laboratory and resulting larvae were evaluated for their growth rates and survival skills. At days 1, 3, 6, 11, and 17 after hatching, larvae were removed from their rearing tanks and their lengths were measured. Day 3 larvae had just completed yolk absorption and were labeled as “yolk” larvae. The oil globule had been completely absorbed by day 6, and these larvae were labeled as “oil” larvae. Days 11 and 17 larvae marked 4 and 11 days after oil absorption, subsequently these larvae were labeled “oil+4” and “oil+11.”

Larval fish from each of the age classes (yolk, oil, oil+4, oil+11) and from control, low- and high-dose MeHg treatments were evaluated for routine behavior and their responses to artificial startle stimuli using video-taped recordings (Alvarez et al., 2006). The video-taped behavior was viewed and the routine behaviors of swimming speed (mm s⁻¹), active swimming speed (mm s⁻¹), net-to-gross displacement ratio (linearity of the swimming path of the larvae), and percent activity were recorded for each larva in each of the four age groupings under control, low- and high-dose treatments. Each individual larva was then subjected to a visual startle stimulus and a vibratory startle stimulus, and the video-taped recording was analyzed to quantify responsivity (percent of larvae responding to the stimulus), response distance (mm), response duration (s), average response speed (mm s⁻¹), maximum response speed (mm s⁻¹), and visual reactive distance (mm). In these experiments, MeHg had no effect on growth rates (mean lengths), but resulted in slower swimming speeds that were statistically significant from control values for the yolk and oil+4 ages; swimming speeds were 23% and 61% slower for low and high doses respectively for yolk.
larva and for the oil+4 larvae were 63% and 59% slower for low and high doses, respectively. The visual reactive distances were slightly reduced, but not significant, for yolk (34% shorter for low dose and 10% shorter for high dose) and oil+4 larvae (17% shorter for low dose and 16% shorter for high dose). For the MeHg-exposed oil larvae the visual reactive distances were 38% and 64% longer for low and high doses respectively but were also not significantly different from control. The MeHg-exposed oil+11 also showed subtle differences that were not significant; low-dose larvae had 23% longer visual reactive distances and high-dose larvae had visual reactive distances that were 5% shorter (Fig. 1). We used swimming speed directly in the IBM to affect encounter rates of larvae with their zooplankton prey and their predators; swimming speed and reactive distance were used with the results of another analysis to estimate how MeHg would affect the probability of the larva escaping an attack by a predatory fish.

2.3. Swimming speeds and probabilities of escape

We adapted a previously developed regression tree model, and used the modified model to relate croaker larva swimming speed and reactive distance to the probability of escaping an attack from a real predatory fish. The original regression tree was based on an experiment involving red drum larvae (same family as croaker), where routine skills and predator-evasion skills in response to an artificial and to a real predatory fish were used (Fuiman et al., 2006). Regression trees are constructed by recursively partitioning data into a hierarchical succession of nodes or branches based on the observed values of a set of predictor variables. The benefits of regression trees over traditional regression techniques are that it is not necessary to assume a linear relationship over the entire range of data (Breiman et al., 1998). Fuiman et al. (2006) fitted a regression tree model to the results from a larval red drum experiment that measured the probability of escape from a real predatory fish for each individual red drum larva \( P(\text{escape}) \), weighted by the number of attacks, as the response variable, and a suite of survival skills (e.g., visual reactive distance) also measured on the individual red drum larva as the predictor variables. We used the same regression tree model as Fuiman et al. (2006), but reduced the number of predictor variables to swimming speed and visual reactive distance because these variables were available in the croaker experiment. The predictor variables developed for red drum were transformed (normalized) so they could be used for croaker larvae (Fig. 2).

The red drum regression tree was converted to a croaker regression tree using \( z \)-scores (standard normal deviates). Swimming speed of red drum was log-transformed for normality, and then the transformed swimming speed and reactive distance were converted to \( z \)-scores and the reduced regression tree was re-fit to the red drum experimental data (Fig. 2). To apply the reduced regression tree to data on croaker larvae, \( z \)-scores were computed from the square-root transformed swimming speeds and Box–Cox transformed visual reactive distances of measured on the croaker larvae (\( \lambda \) of 0.4; SAS Version 9, SAS Institute Inc., USA), and these were inputted into the reduced regression tree based on red drum that used \( z \)-scores. Probabilities of escape were predicted for each croaker larva from the swimming speeds and reactive distances measured for each age grouping (yolk, oil, oil+4, and oil+11) and for the control, low- and high-dose MeHg exposures.

Swimming speeds and regression tree-predicted probabilities of escape were then expressed as multipliers and used in...
Fig. 3. Mean values of swimming speed (mm s\(^{-1}\)) and probability of escape, and frequency histograms of their multipliers, by age-grouping for control, low- and high-dose MeHg treatments used in the IBM. Age groupings were: (A) day 3 or yolk just absorbed, (B) day 6 or oil globule just absorbed, (C) day 11 or 4 days past oil globule absorption, (D) day 17 or 11 days past oil globule absorption. The probability of escape multipliers were derived via the regression tree. Multipliers were created by dividing each swimming speed and probability of escape value for each age grouping (days 3, 6, 11 and 17) and treatment (control, low or high) by the mean of the swimming speed or probability of escape for the control for its age grouping. Arrows point to treatment group for the mean swimming speeds and probability of escapes; means are ordered as high dose to left, low dose in the middle, and control to right in each panel.

The multipliers by age grouping were obtained by dividing each swimming speed and probability of escape by the mean value for control larvae in its age grouping for control, low- and high-dose MeHg treatments (Fig. 3). Swimming speed multipliers were generally reduced in the low- and high-dose MeHg exposures relative to control swimming speed multipliers. The effect of MeHg on the probability of escape multipliers was not as clear; probability of escape multipliers were roughly similar for yolk age larvae for all treatments, and slightly lower for oil and oil+4 age larvae for the low and high MeHg treatments and lower for oil+11 larvae for the high dose. Swimming speed and probability of escaping multipliers were randomly assigned to each larva in the IBM and used with that larva until it entered the next age grouping, when a new set of multipliers was randomly assigned to the larva from the next age’s histogram.

Fig. 4. Schematic diagram of the individual-based model larval cohort model. The IBM simulates the daily growth and mortality of ocean larvae as they grow from 2.5 to 11 mm. Growth is based on bioenergetics principles, with ingestion dependent on encounter rates of larvae with four types of zooplankton. Mortality was based on the encounter and capture of larvae by individual medusae, ctenophores, and predatory fish. MeHg influenced larval swimming speed, which affected encounter rates of larvae with zooplankton and with predators, and influenced the probability of escaping a predatory fish attack (after Rose et al., 2003).

2.4. Individual-based model

The IBM tracked the daily growth and mortality of a cohort of Atlantic croaker larvae from 2.5 to 11 mm in a 20,000 m\(^3\) volume of water (Fig. 4), and was used to predict ocean larval-stage survival and duration for the control, low- and high-dose MeHg treatments. The treatments differed by the swimming speed and probability of escape multipliers assigned to larvae for each age grouping. The model began with 10,000, 2.5-mm larva, assumed densities of four prey groups (invertebrate eggs, nauplii, copepodites and adult copepods; see Table 1), and some number and assigned sizes of individual predators (medusa, ctenophores and fish). Larval growth rate each day depended on their encounters with and captures of the zooplankton prey, and their mortality rate depended on their encounters with and escape from individual predators. MeHg effects on swimming speed affected larval encounters with zooplankton and predators; MeHg effects on the probability of escape affected the ability of larvae to escape predatory fish attacks.
Inversion was determined by simulating the foraging of a larva via its encounters, captures, and diet selection with four types of zooplankton prey. The four prey types were defined by their length, weight, and density (Table 1). All four prey items were found in stomachs of larval Atlantic croaker shorter than 10 mm (Govoni et al., 1983, 1986).

Daily encounter rates of each larva with each individual prey type (number of encounters per day) were a product of the larval search volume (SV, mm$^3$ s$^{-1}$), density of the prey type ($\rho$, Table 1), and the number of seconds in 13 h of presumed daylight (46,800):

$$ER_{\text{preytype}} = SV \times \rho \times 0.001 \times 46,800$$

Multiplication by 0.001 converts mL to mm$^3$. Search volume was the product of the swimming speed of the larval fish (SS, mm s$^{-1}$) and its reactive area (RA, mm$^2$):

$$SV = SS \times RA$$

Swimming speed was dependent on length of the fish, and averaged about 1 body length/s (Miller et al., 1988):

$$SS = 0.776 \times \text{length}^{1.07}$$

Reactive area was a half circle with radius equal to the reactive distance (RD, mm) defined for each prey type and larva:

$$RA = (RD_{\text{preytype}})^2 \times \pi \times 0.5$$

Reactive distance increased with prey length and with predator length because longer larvae have smaller angles of acuity (Breck and Gitter, 1983):

$$RD_{\text{preytype}} = \frac{\text{length}_{\text{preytype}}}{2 \tan(\alpha/2)}$$

where $\alpha$ is the minimum angle that resolves a prey item from the background. $\alpha$ decreased with larval length:

$$\alpha = 0.0167 e^{9.14-2.4 \ln(\text{length})+0.229 (\ln(\text{length}))^2}$$

The realized number of encounters in 13 h (ER(realized)) was calculated as a random deviate from a Poisson distribution with mean and variance equal to the mean encounter rate (ER$_{\text{preytype}}$). Realized encounter rates were computed daily between each larva and each of the four zooplankton prey types.

The number of each prey type encountered that were subsequently captured and ingested was determined based upon capture success, a diet selection algorithm, and a maximum consumption rate. Croaker larvae consume larger prey at a given size

Table 1: Length (mm), weight (µg), and density (number mL$^{-1}$) for each of the four zooplankton prey types used in the IBM

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Length</th>
<th>Weight</th>
<th>Density</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Invertebrate  eggs</td>
<td>0.11</td>
<td>0.250</td>
<td>0.3</td>
<td>Length and weight based on the sizes of copepod eggs reported in Kiorboe and Sabatini (1994)</td>
</tr>
<tr>
<td>Nauplius</td>
<td>0.25</td>
<td>0.282</td>
<td>0.08</td>
<td>Length and weight from Letcher et al. (1996)</td>
</tr>
<tr>
<td>Copepodite</td>
<td>0.5</td>
<td>1.410</td>
<td>0.008</td>
<td>Length and weight from Letcher et al. (1996)</td>
</tr>
<tr>
<td>Copepod</td>
<td>1.0</td>
<td>7.700</td>
<td>0.0008</td>
<td>Weight from Letcher et al. (1996) assuming a 1-mm length copepod because larval croaker eat relatively large copepods compared to most marine larvae (Govoni et al., 1986; Rose et al., 2003)</td>
</tr>
</tbody>
</table>

Densities were initially estimated from data reported in plankton surveys conducted offshore in the Gulf of Mexico (Al-Yimani, 1988) and in the mid-Atlantic Bight (Kane, 2003), and then were slightly adjusted to obtain realistic larval growth.

2.4.1. Growth

The growth component of the IBM was a foraging and bioenergetics model adapted from a generic marine larval model described by Letcher et al. (1996). We adjusted the temperature-dependent rates in the model of Letcher et al. (1996) to apply to 15 °C. This is typical water temperature experienced by ocean larvae in the mid-Atlantic Bight, which is an area of high croaker abundances (Stegmann et al., 1999). All equations for the foraging and bioenergetics model came from Letcher et al. (1996) unless noted otherwise.

Daily change in weight ($W$) of an individual larva was computed as

$$\Delta W = W_{t+1} - W_t = AI - M - E$$

where $A$ is the assimilation efficiency, $I$ is the ingestion ($\mu g$ day$^{-1}$), $M$ is the total metabolic cost ($\mu g$ day$^{-1}$), and $E$ is the combined losses due to excretion and specific dynamic action. Each day, weight was converted to length for each larva using a length–weight relationship:

$$W = 0.1674 \times \text{length}^{3.837}$$

The length of the larva was updated if the weight gain was positive and the larva had reached at least the average weight expected for its length.

The combined excretion and specific dynamic action term ($E$) was assumed to be 30% of ingestion, and assimilation efficiency and metabolism depended on fish weight. Assimilation efficiency increased from a minimum of 0.45 at a weight of 1658 µg to a maximum of 0.6 at a weight of 45,000 µg:

$$A = 0.6((1 - 0.25 e^{-0.002(W-10)})$$

We lowered the maximum assimilation efficiency to 0.6 from Letcher et al.’s value of 0.8 because croaker larvae grow slower than the generic larva simulated in Letcher et al.’s (1996) model (Nixon and Jones, 1997). Total metabolic cost ($M$) included a routine component plus an active component that was 2.5 times the routine component for daylight hours:

$$M = \frac{4500W}{45,000 + W} + 2.5 \times \left( \frac{4500W}{45,000 + W} \right) \times \text{light}$$

where light is the number of hours of daylight (assumed to be 13) and 4500 and 45,000 are parameters that were empirically derived by Letcher et al. (1996) and were based upon laboratory-measured rates of metabolism from several species of larval fish.

In the routine component for daylight hours: $\text{light} = 4500 + 45,000$ is the total metabolic cost ($\mu g$ day$^{-1}$). Total metabolic cost ($M$) included the background: $\text{light} = 4500 + 45,000$ for both $M$ and $E$.
than typical marine larvae (Govoni et al., 1983, 1986; Soto et al., 1998; Rose et al., 2003). Therefore, capture success functions of Letcher et al. (1996) were altered to have higher capture probabilities (Fig. 5). Capture success was used in the diet selection algorithm to determine which prey types were eaten. For each larva on each day, handling time (Walton et al., 1992) was first computed:

$$HT_{preytype} = e^{0.264 \times 10^{7.0151 (preytype/length/length)} }$$ (11)

Then handling time and capture success were combined to obtain mass per unit time for each prey type:

$$mass_{preytype} \times CS_{preytype} \over HT_{preytype}$$ (12)

Prey types were ordered from highest to lowest based on their mass per unit time. The profitability (defined as the ratio of energy consumed of each prey type divided by the time required for handling those prey) of each prey type was also computed:

$$\text{energy}_{preytype} \over \text{time}_{preytype} = \sum_{preytype} \text{mass}_{preytype} \times \text{ER(realized)}_{preytype} \times \text{CS}_{preytype} \over 1 + \sum_{preytype} \text{ER(realized)}_{preytype} \times HT_{preytype}$$ (13)

Prey types were evaluated in order of their mass per unit time, and types were included in the diet until profitability began to decrease. The number of prey items of each type included in the diet was then determined by generating a random deviate from a binomial distribution, with number of trials equal to the realized encounter rate per day (ER(realized)) and with probability of success equal to capture success (CS). Maximum consumption depended on larval weight:

$$C_{max} = 2.8275 W^{0.8496}$$ (14)

Prey items were multiplied by their weight (Table 1) and added to the cumulative biomass ingested according to the ordering of the profitable types, as long as ingestion did not exceed maximum consumption.

2.4.2. Starvation

Starvation mortality occurred when a larva’s weight went to less than 25% of its maximum weight achieved to date in the simulation. Weight loss predicted by the bioenergetics model was adjusted using the same algorithm as Letcher et al. (1996) so that when fed nothing, a larval croaker at 2.5 mm total length would starve to death after roughly 5 days.

2.4.3. Mortality by predation

Mortality by predation occurred when larvae were encountered and captured by any of the ctenophore, jellyfish medusae, or predatory fish individuals (Cowan et al., 1996; Rose et al., 2003). Numbers of individuals of each predator type in the modeled volume were specified, and lengths were randomly assigned to each individual predator from normal probability distributions (Table 2; Cowan et al., 1996). On each day of the simulation, the model used a modified Gerritsen–Strickler formulation (Bailey and Batty, 1983) to compute the encounter rate of each larva with each individual of the three predator types:

$$ER_{predatortype} = \pi (R_L + R_p)^2 \left( \frac{10^{-9}}{V} \right)$$ (15)

where ER is the encounter rate of a larva with an individual predator (number of encounters in 24 h), $R_L$ is the encounter radius of larva (mm), $R_p$ is the encounter radius of the predator (mm), $C$ is the foraging rate (mm s$^{-1}$), and $V$ is the volume of water modeled in the simulation (20,000 m$^3$). The encounter radius of larva was computed from larval length (mm) as

$$R_L = \frac{2 \times \text{length}}{\pi^2}$$ (16)

The encounter radius of each predator type was derived from laboratory studies (Table 2). The foraging rate ($C$) was determined as

$$C = \begin{cases} \frac{D_L^2 + 3D_p^2}{3D_p}, & \text{if } D_p > D_L \\ \frac{D_p^2 + 3D_L^2}{3D_L}, & \text{if } D_p < D_L \end{cases}$$ (17)

where $D_L$ is the distance swum in a day by a larval fish (mm) and $D_p$ is the distance swum in a day by a predator (mm). The distance swum in a day by a larval fish was calculated by

$$D_L = SS \times 46,800$$ (18)

where 46,800 is the number of seconds in 13 h because larval fish were assumed to be active only during the day (Kjelson et al., 1975). This assumption restricts the amount of time larval fish use to capture enough prey to sustain growth, but also reduces encounters with predators. $SS$ is the swimming speed of the larval fish (Eq. (7)). The calculation of $D_p$ depended upon the swimming speeds of the predators, which in turn depended upon the lengths for each of the three predator types (Table 2). Predators were assumed to be active for all 24 h in a day. Medusae and ctenophores are active throughout 24 h. In natural systems medusae and ctenophores may migrate vertically in concert with
daylight (e.g., Mills, 1983) but we do not incorporate this spatial complexity in our model. We also simulated a generic fish predator that could be either nocturnal or diurnal.

The realized number of encounters between a larva and each individual predator was generated as a random deviate from a Poisson distribution with mean equal to the mean encounter rate (\(ER_{\text{predatortype}}\)). The number of successful realized encounters with that predator individual was then randomly drawn from a binomial distribution with the probability of success equal to the capture success for that predator type using the predator and larval lengths (see Table 2). On each day, each larva’s encounters and potential capture were evaluated for all of the individual predators. If a larva was successfully encountered and captured by any of the individual predators of any of the three predator types, that larva was considered eaten and was removed from the simulation. Individual predators were evaluated in random order each day so that we could fairly assign each larva eaten to a predator type and interpret the percent of mortality caused by ctenophores, medusae, and predatory fish.

### 2.4.4. MeHg effects on growth and predation mortality

Each larva in the simulation received a new set of multipliers for swimming speed and probability of escape on the day they entered each age grouping (yolk, oil, oil+4, oil+11) from the control, low- or high-dose histograms (Fig. 3). The multipliers were randomly assigned to each larva from the histograms without regard to multipliers previously assigned to that larva (i.e., no memory in the multipliers). Swimming speed (Eq. (5)) which, in turn, affected the encounter rate of the larva with each zooplankton prey (\(ER_{\text{preytype}}\), Eq. (5)). Swimming speed also affected the larva’s distance swum (\(D_L\), Eq. (18)), which affected the foraging rate (\(C\), Eq. (17)) which, in turn, affected the larva’s encounter rate with each of its predators (\(ER_{\text{predatortype}}\), Eq. (15)). The probability of a larva being captured by a predatory fish was adjusted by converting the probability of capture to the probability of escape (\(P_{\text{escape}} = 1 - P_{\text{capture}}\)), applying the multiplier for probability of escape, and then re-computing the probability of capture. Multipliers were only applied to larval encounters with individuals of the predatory fish because the red drum laboratory study that provided the regression tree, only examined predatory fish. Also, predatory fish are able to see larval fish and attack them, whereas medusae and ctenophores encounter larval fish passively.

### 2.5. Simulations

Two sets of model simulations were performed to explore the effects of MeHg on ocean larval-stage duration and survival. The first set (six simulations) involved baseline (control), low- and high-dose MeHg swimming speed and probability of escape multipliers under a medusa-dominated and a fish-dominated predator mix. These simulations were designed to assess the overall impact of MeHg exposure on stage duration and survival.

The second set of simulations (eight simulations) repeated the low- and high-dose MeHg simulations under the two predator compositions of the first set but with MeHg effects imposed on growth only and with MeHg effects imposed on predation only. The objective of the second set of simulations was to determine the relative contribution of growth and predation mortality to overall effect of MeHg on stage duration and survival predicted in the first set of simulations. Under growth only, MeHg-derived swimming speed multipliers affected larval encounters with zooplankton; control-derived multipliers of swimming speed and probability of escape were used to simulate encounters with predators. Under predation only, control-derived swimming speed multipliers affected larval encounters with zooplankton, while MeHg-derived swimming speed multipliers affected larva encounters with all predators and MeHg-derived probability of capture multipliers affected the capture success of predatory fish encounters.

The two predator mixes were designed to reflect two possible predator communities an ocean larva might encounter. For the medusa-dominated mix, we assumed there were 1185 medusae, 355 ctenophores, and 46 individual juvenile fish in the 20,000 m³ volume. These numbers of predators were roughly consistent with lowered densities tilted more towards medusae than those used by Cowan et al. (1996) for their Chesapeake Bay...
application. Predators are generally found in lower densities in offshore environments (e.g., Gulf of Mexico, SEAMAP, 2001, 2002; California current, Suchman and Brodeur, 2005), and offshore trawls in the Gulf of Mexico and North Atlantic during late fall and early winter indicated that medusae were at higher concentrations than ctenophores (SEAMAP, 2001, 2002; Link et al., 2006). The medusa-dominated predator numbers produced appropriate mortality rates estimated for Atlantic croaker ocean larva (i.e., stage survival of 0.9–1.7%; Diamond et al., 1999, 2000). The fish-dominated mix increased the number of predatory fish and reduced the number of medusa (45 medusae, 355 ctenophores, and 9000 juvenile fish) to reflect larvae experiencing high densities of predatory fish; predicted stage survival was similar (about 1.1%). The medusa-dominated mix was based on field data and considered realistic, while the fish-dominated mix had very high predatory fish densities in order to provide a contrast to the medusa-dominated mix.

Three replicate simulations that used different random number sequences were performed for each of the conditions. Baseline results are shown in more detail than the other conditions to illustrate several auxiliary outputs of the model aside from stage duration and survival (e.g., diets, length frequency histograms through time, mean lengths of live and dead larvae) and for clarity in some tables and figures, we only show results for one of the replicate simulations. Because of the high variance in larval lengths at snapshots during the simulation, larvae ranging in total length from 3 to 10 mm were present on some days during the simulation. We therefore summarized some information (diets, mean growth rates, and mean mortality rates) based on larval length, rather than time (age), in order to reduce variability and more clearly show patterns. Model predictions were very similar among the three replicate simulations for each condition simulated. Predicted larval-stage survival (%) and duration (days) are presented as the average (with ±S.D. error bars) based on the three replicate simulations.

3. Results

3.1. Baseline simulations

Predicted larval-stage duration and stage survival differed slightly between baseline simulations that used the medusa-dominated predator mix versus the fish-dominated predator mix. Predicted stage survival and duration for the three replicate simulations was 1.1, 1.0, and 1.0% and 30.7, 29.0 and 29.7 days for the medusa-dominated predator mix, and 0.9, 1.1, and 1.3% and 32.5, 33.9, and 34.7 days for fish-dominated predator mix.

Detailed examination of a single replicate baseline simulation under the medusa-dominated predator mix showed that prey size and growth rates increased with larval length, and that mortality was size-independent (Fig. 6). Very small larvae (about 3 mm) tended to eat the smaller sized zooplankton groups; copepods dominated the diet of 6 mm and longer larvae (Fig. 6A). Length–frequency distributions showed that individuals exhibited highly variable growth rates (Fig. 6B). The predicted length distribution was very broad by day 20, with some individuals having exhibited little growth and others having reached 11 mm.

By days 40 and 60 of the simulation, the length frequencies were irregular, with a significant proportion of the survivors still shorter than 4 mm. Growth rates were very slow in the first few days of feeding when larvae were about 3 mm in length, and they rapidly increased for those that survived this initial period of first feeding (Fig. 6C).

Daily mortality rates were 0.1–0.2 day⁻¹, and remained relatively constant with larval length (Fig. 6D), with no clear difference between mean length of surviving individuals and those that died each day (Fig. 6E). The rapid decline in the number of survivors over time was due to predation (60% of all deaths) and starvation (39% of all deaths) with 87% of the predation deaths caused by medusae, 12% by predatory fish, and 1% by ctenophores (Fig. 6F). Starvation mostly occurred during days 6–10, reflecting the lag in death by starvation created by the adjusted rate of weight loss in poorly feeding larvae.

Baseline simulations with the fish-dominated predator mix generated similar growth-related results and total survival as those with the medusa-dominated predator mix, but differed in the causes of the mortality (Fig. 7). The growth processes were not affected by changing the predator composition; therefore, larval fish diet (Fig. 7A), length distributions with time (Fig. 7B), and growth rates (Fig. 7C) showed a very similar pattern to that predicted under the medusa-dominated mix. As expected, because we adjusted the number of individuals of each predator type, predicted stage survival was also about 1–2%.

The fish-dominated predator mix differed from the medusa-dominated composition in that mortality rate became more strongly size-selective and more deaths resulted from fish predation and less from starvation (Fig. 7). Daily mortality rate generally decreased with larval length (Fig. 7D), and during days 10–30 the mean lengths of surviving larvae were generally longer than those that died on each day (Fig. 7E). Predation still dominated mortality (85% of all deaths), but under the fish-dominated composition 81% of those eaten were consumed by predatory fish, 17% by medusae, and only 14% of the total mortality was due to starvation (Fig. 7F). The high density of fish predators caused higher fish predation that was size-selective, which removed shorter individuals before they succumbed to starvation.

3.2. Effects of MeHg

Methylmercury reduced stage survival and increased stage duration similarly for the medusa-dominated and fish-dominated predator mixes (white, grey, and black solid bars in Fig. 8). Averaged stage survival under the medusa-dominated predator mix was 0.19% (19% of the 1% survival in baseline) for the low dose and 0.07% (7% of baseline) for the high dose, and was about 0.15–0.16% for both doses under the fish-dominated predator mix. Averaged stage durations under the medusa-dominated predator mix were 32.7 days (2.9 days more than baseline) for the low dose and 34.1 days (4.3 days more than baseline) for the high dose, and under the fish-dominated predator mix were 34.6 days (0.9 days more than baseline) for the low dose and 37.7 days (4 days more than baseline) for the high dose. The high-dose MeHg exposure caused larger reductions in survival
Fig. 6. Results from a single replicate simulation under baseline (control) conditions with the medusa-dominated predator mix. We show results for one baseline simulation to illustrate several auxiliary outputs of the model aside from stage duration and survival. (A) Mean biomass of the four zooplankton prey types consumed by length class of larvae expressed as a percent of total biomass consumed, (B) length frequency distributions of larval fish at days 1, 10, 20, 40 and 60, (C) mean growth rate (±S.D.; mm day$^{-1}$) by length class of live larvae, (D) mean mortality rate (±S.D.) by length class of dead larvae, (E) mean length of live larvae and dead larvae each day, and (F) numbers surviving (left axis) and cumulative number eaten by predator type (right axis).

and greater increases in stage duration than the low dose (i.e., hint of a dose–response relationship), except for survival under the fish-dominated predator mix for which survival was similar between the low and high doses.

While MeHg effects on stage survival and duration were similar between the medusa-dominated and fish-dominated predator mixes, the causes of increased mortality differed between the predator mixes (Table 3). MeHg exposure caused increased starvation under the medusa-dominated predator mix, whereas predation played a more important role with the fish-dominated predator mix. In the medusa-dominated predator mix, the low and high MeHg doses resulted in fewer individuals being eaten (48.1% and 47.8% versus 62.8% in baseline) and more individuals starving to death (51.7% and 52.0% versus 36.1% in baseline). In the fish-dominated predator mix, low dose of MeHg caused increased predation (90.2% versus 85.6% in baseline),

<table>
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<tr>
<th>Predation scenario</th>
<th>Control (%)</th>
<th>Low MeHg (%)</th>
<th>High MeHg (%)</th>
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<tr>
<td></td>
<td>Predation</td>
<td>Starvation</td>
<td>Predation</td>
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<tr>
<td>Medusa dominated</td>
<td>62.8</td>
<td>36.1</td>
<td>48.1</td>
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<tr>
<td>Predatory fish dominated</td>
<td>85.6</td>
<td>13.1</td>
<td>90.2</td>
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The percents are the average values over the three replicate simulations.
which more than offset the decrease in starvation (9.6% versus 13.1% in baseline) resulting in reduced overall survival. In the high-dose treatment, predation only decreased slightly (83.9% versus 85.6% in baseline) and starvation increased slightly (15.8% versus 13.1% in baseline) resulting in an overall effect of reduced stage survival.

MeHg effects on growth dominated the response of stage survival and duration under the medusa-dominated predator mix, while MeHg effects on mortality by predation played a more important role under the fish-dominated predator mix (dotted and hatched bars in Fig. 8). Under the medusa-dominated predator mix (top panels), predicted stage survival and stage duration with MeHg effects on growth only were very similar to those predicted when MeHg effects were imposed on both growth and mortality. Indeed, under the medusa-dominated predator mix, imposing low- and high-dose MeHg effects only on mortality actually resulted in an increase stage survival, and very little changes in stage duration. The MeHg effect on the probability of escape was only applied to the predatory fish. With the relatively few fish in the medusa-dominated mix, MeHg effects on the probability of capture were inconsequential. Mortality effects alone involved slower swimming speeds that caused fewer encounters with predators and therefore created a small increase in stage survival. The response for the medusa-dominated predator mix was determined almost completely by slower swimming speeds, which resulted in fewer encounters with zooplankton prey and therefore slowed growth. Slower growth rates, combined with size-independent mortality rates under the medusa-dominated predator mix, caused longer stage durations and higher cumulative-stage mortality.

MeHg effects on predation mortality played a more important role in the fish-dominated predator mix (dotted and hatched bars in bottom panels in Fig. 8). The larger number of predatory fish in the fish-dominated predator mix amplified the effects of
MeHg on the probability of escape of the larvae. Predicted survival for the predation mortality effects alone was 0.27% for the low dose (31% of baseline) and 0.13% (58% of baseline) for the high dose. Higher survival occurred under the high dose compared to the low dose because the very slow swimming speeds under the high dose reduced encounters that, to some degree, counteracted the slightly lower probabilities of escape. MeHg effects on growth only with the fish-dominated predator mix reduced survival and increased duration about the same as with the medusa-dominated predator mix. With the fish-dominated predator mix, MeHg effects on mortality somewhat offset the effects on growth. Expected survival if mortality and growth operated independently was 4% for the low dose (0.31 of baseline from mortality alone times 0.13 of baseline from growth alone) and 3% (0.58 × 0.05) for the high dose. Actual stage survivals when mortality and growth effects were imposed together (14% for low dose and 15% for high dose) were higher than expected under complete independence. Size-selective aspects of mortality under the fish-dominated predator mix culled slow growing larvae, reducing to some extent the effects of a slower growth on mortality.

4. Discussion

We used a non-traditional statistical method (regression tree) and an individual-based larval fish cohort model to scale MeHg effects on behavior to changes in the larval-stage survival and duration of Atlantic croaker. The results of laboratory experiments on Atlantic croaker and red drum were combined to relate a low and high MeHg exposure to swimming speeds and probability of a larva escaping a predatory fish attack. Using results measured on red drum for croaker was partially justified as they both belong to the same Sciaenidae family. MeHg-derived effects on swimming speeds and probability of escape for the low and high dose were determined for four age groupings of croaker larvae and imposed on simulated larval individuals in the IBM. Because swimming speeds affect larval encounters with their zooplankton prey and with their predators, both the low and high doses resulted in large reductions in stage survival and increases in stage duration, and these responses were similar for two alternative mixtures of predators (medusa-dominated and fish-dominated). Given that the effects of the probability of escape were only imposed on predatory fish attacks, the causes of the increased mortality depended on the type of predator mix. MeHg exposure caused slowed growth and increased starvation under the medusa-dominated predator mix, whereas both growth and predation mortality were affected by MeHg with the fish-dominated predator mix.

As expected, both predator mixes generated similar reductions in stage survival. We adjusted the number of fish individuals in baseline simulations with the fish-dominated mix to roughly match the 1% survival obtained with the medusa-dominated predator mix. While the densities of predators in the medusa-dominated mix were grounded in field data and likely realistic, we needed many fish individuals in the fish-dominated mix to get both size-dependent mortality and the desired 1% survival under baseline conditions. Sustained exposure of croaker larvae to 0.9 predatory fish m⁻³ seems extreme, but predator densities as high have been reported previously (0.875 blueback herring predators m⁻³; Chick and Van Den Avyle, 2000). However, densities of blueback herring predators in freshwater reservoirs are likely to be higher than densities of juvenile predatory fish in the open ocean. We opted for the high predatory fish density because MeHg effects on growth were dominant in the medusa-dominated mix and we wanted an alternative mix in which mortality was more size-dependent and MeHg effects on predation mortality (via changes in probability of escape) were more likely to be important. Contrasting the medusa-dominated and fish-dominated mixes showed the complexity of how contaminant effects on swimming speeds...
and predator evasion get combined in the IBM in a series of non-linear encounter and capture calculations that depend on characteristics specific to the predator types (Table 2). For example, medusae showed no significant selection for prey size (Fig. 7D), whereas juvenile predatory fish were size selective (Fig. 7D). Our results explore how the effects of a contaminant on behavior documented in the laboratory (e.g., reduced probability of escape) can contribute to survival in the field and that the outcome is dependent on the types of predators and their abundance.

The realism of the predicted effects of MeHg exposure in this analysis is conditional on the realism of the IBM. The baseline IBM simulation results were all reasonable (Figs. 6 and 7) and similar patterns with larvae fish have been shown in the laboratory and natural settings. Highly variable growth rates that generally increase with size have been reported in laboratory settings. Cohorts of fish reared in the laboratory and in large enclosures that had the same birth date showed high variability in growth rates (Fuiman et al., 2005), and RNA/DNA ratios (a measure of protein synthesis) generally increase with larval size or age (Buckley, 1982, 1984). The sensitivity of larvae to poor growth during the first few days of exogenous feeding predicted by the IBM has also been widely reported. Most species of larval fish are known to have difficulties with capturing prey during the period of time when larval fish switch from endogenous to exogenous food sources (Hjort, 1914; Ware et al., 1981; Blaxter, 1986), and starvation is a serious risk during this period because of high mass-specific metabolic rates and the low energy reserves typical of fish larvae (Fuiman, 2002). Robinson and Ware (1988) used RNA/DNA ratios and calculated a window of time of about 6 days after which unfed larval herring attained irreversible starvation. Finally, the shifts to larger prey with size and age have been documented for croaker larvae. First feeding croaker larvae eat small zooplankton, and switch to mostly larger copepods after 6 mm in length (Govoni et al., 1983, 1986; Soto et al., 1998; Rose et al., 2003).

The relatively large contribution of starvation to mortality in baseline simulations was unexpected. In the IBM, slight variation in metabolic rates or in the parameters controlling death by starvation (i.e., adjustment to weight loss; 25% of maximum weight threshold) had large effects on whether a simulated larval fish died from predation or starvation (Letcher et al., 1996). Our more realistic medusa-dominated predator mix resulted in almost 35% of the initial larvae dying from starvation, which seemed high; the more contrived fish-dominated mix resulted in a more realistic 13%. Starvation has been suggested to be one of the main causes of mortality in marine fish larvae (Cushing, 1974; Lasker, 1975; Leggett and Deblois, 1994), although many believe that in nature weak larvae usually get eaten before succumbing to starvation (Cushing, 1974; Hunter, 1981). Laboratory studies on related species and field-based studies on Atlantic croaker suggest that larval croaker are relatively vulnerable to starvation. Laboratory studies using RNA/DNA ratios for larval red drum, a related species, demonstrated that red drum have a critical period (switch to exogenous feeding) during which starvation is a serious risk (Westerman and Holt, 1994). Otolith studies on Atlantic croaker suggest that larvae spawned in September and October in the mid-Atlantic Bight experience falling plankton abundance and have slow growth rates that make them prone to starvation (Nixon and Jones, 1997). Additionally, field-caught newly settled estuarine Atlantic croaker have much higher percentages of empty stomachs than other settling larvae (Govoni et al., 1983), suggesting that by the end of the larval period, Atlantic croaker larvae have nearly exhausted their stored energy reserves. With cumulative mortality so high in our model simulations, the proper balance between starvation and predation may not greatly affect predicted stage survival (slow growing larvae would ultimately get eaten if they did not starve). However, prediction of stage survival and duration from application of the IBM to other life stages (e.g., juveniles) and with more dilute predator mixes can be sensitive to the relative importance attributed to starvation versus predation.

In addition to potential errors introduced from an unrealistic IBM, two other sources of potential uncertainty were how we dealt with the age groupings in simulations and the use of a red drum experiment to infer how the probability of escape of croaker would be affected by MeHg exposure. Although imposing age-group specific multipliers of swimming speed and probability of escape was easy within the structure of the IBM, multipliers assigned to a larva in one age group did not influence the multipliers it received when it went to the next age group. We did this to mimic the laboratory results where only the MeHg effects on behavior of an individual within each single age grouping were tracked. This meant that in model simulations an individual fish that had above average multipliers assigned at one age grouping (i.e., a fast swimmer) was equally likely as another individual to be assigned below average multipliers (i.e., slow swimmer) when it entered the next age grouping. Additional simulations could assume a correlation in the multipliers of an individual from age group to age group; performing the analogous laboratory experiments would be a challenge. Additional experiments that used croaker, rather than red drum, in trials with a real predatory fish and with medusa and ctenophore predators would also help refine the regression tree and the assignment of swimming speed and probability of escape multipliers in model simulations.

Our analysis has some similarities to the analysis of growth rates on larval striped bass survival reported by Chick and Van Den Avyle (2000). They grew striped bass larvae in the laboratory under different prey densities and video-taped their swimming speeds and responsiveness to predatory fish for use in a larval cohort model. Chick and Van Den Avyle (2000) simulated two alternative predatory fish in their model and concluded that behavioral differences among the growth rate (prey density) treatments had little effect on predator encounters but that slowed growth lead to higher cumulative mortality. The authors found some differences between their two fish predator species. We also found that swimming speed can affect survival via growth more than by directly affecting predation mortality, but we found this with a predator mix dominated by medusae. Stage survival actually increased slightly over baseline when MeHg effects on swimming speed and probability of escape were only applied to the predators under the medusa-dominated predator mix (Fig. 8).
However, when MeHg effects were applied to growth alone and to both growth and mortality, stage survival decreased (Fig. 8). When we used the fish-dominated predator mix and imposed MeHg effects on mortality only, stage survival was about a 50% lower than baseline. Despite the similar approaches and models used by us and by Chick and Van Den Avyle (2000), these differences illustrate how the details assumed about the predators can greatly affect behavioral effects on survival.

The relevance of our simulation results to field conditions depends on the realism of the MeHg exposures used in the laboratory experiments, and whether we simulated the major effects of MeHg exposure on larvae that would occur in nature. Direct field evidence in support of MeHg effects on larval croaker growth and survival, as with many species and contaminants, is either equivocal or not available. Most laboratory studies examined growth and survival of fish that were exposed to relatively high MeHg levels. MeHg did not affect growth of laboratory-studied Atlantic croaker (Alvarez et al., 2006), larval and juvenile walleye (Stizostedion vitreum) (Friedmann et al., 1996; Latif et al., 2001), larval fathead minnows (Pimephales promelas) (Hammerschmidt et al., 2002), or zebrafish larvae (Danio rerio) (Samson et al., 2001). However, MeHg decreased feeding and impaired the competitive abilities of grayling (Thymallus thymallus) (Fjeld et al., 1998), reduced prey capture ability and prey capture ability of zebrafish (Samson et al., 2001), reduced swimming ability and prey capture ability of mummichogs (Fundulus heteroclitus; Weis and Weis, 1995a,b; Zhou and Weis, 1998), and reduced the swimming ability of minnows (Kolok et al., 1998).

The low MeHg treatment in the laboratory experiments used here were considered realistic, albeit near the high end, when compared to MeHg levels observed in field-caught fish. If we assume a 10% transfer of MeHg from the body to the eggs (Alvarez et al., 2006), we would back calculate that the female Atlantic croaker treated with low-dose MeHg would have body burdens of MeHg ranging from 14.4 to 31.3 μg g⁻¹ of fish. Such levels are generally about 10-fold higher than average levels observed in the field. For example, values in perch, Perca fluviatilis, and chub, Leuciscus cephalus, were 1.7 and 2.1 μg g⁻¹ in the Elbe River (Marsalek et al., 2006), and were about 1.4 μg g⁻¹ in splendid alfonso, Beryx splendens, and bigeye tuna, Thunnus obesus, from Japan (Yamashita et al., 2005). However, our back-calculated concentrations were similar to maximum observed concentrations reported for species such as Atlantic croaker, spot, Leiostomus xanthurus, sand seatrout, Cynoscion arenarius, and hardhead catfish, Arius felis (e.g., 36.3 μg g⁻¹ in Lavaca Bay, Point Comfort, TX; NOAA Status and Trends Program, http:\/\cmaserver.nos.noaa.gov).

Trying to relate our modeling results directly to field conditions, without further refinement, is setting the bar for success very high. Regardless of whether these model simulations can be interpreted for natural populations, the approach used here is useful for providing a quantitative way to express behavioral effects of contaminants measured in the laboratory to ecologically relevant endpoints of stage survival and stage duration. Such ecological endpoints help in the interpretation of possible risks from behavioral effects, and allow for comparison of these possible risks among different species and contaminants.

5. Conclusions

Combining statistical- and individual-based simulation models provides a framework for relating behavioral effects of contaminants to ecologically relevant endpoints. Our analysis of Atlantic croaker larvae exposed to MeHg showed that slowed swimming speed and reduced probability of escape from a predator attack, documented using video-taped laboratory experiments, may result in reduced larval-stage survival and prolonged stage duration. Details of the causes of the increased mortality depended on the mixture of predator types to which the larvae were exposed. These results were highlighted by the use of statistical and IBM simulations and are not obvious when examining the laboratory results alone. Such changes in larval-stage survival and duration allow for easy comparisons of effects among life stages, species, and contaminants, and can be important to long-term population dynamics. The results of this analysis (changes in stage survival and duration) can be used to change parameters of matrix projection models that are commonly used to model fish populations thereby forging a strong link between behavioral responses to contaminant exposure and long-term population dynamics.

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