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Original Article

The effect of variable winter severity on size-dependent overwinter mortality caused by acute thermal stress in juvenile red drum (*Sciaenops ocellatus*)

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Mortality during winter can impact the population dynamics of fish at temperate latitudes. The red drum (*Sciaenops ocellatus*) supports valuable coastal fisheries throughout its range in the southeastern United States. At the northern edge of its distribution, severe winters may cause considerable overwinter loss and size-selective mortality among juveniles. We conducted a series of laboratory experiments to quantify overwinter survivorship of age 0 fish. To determine thermal tolerance, fish were exposed to various minima (1, 3, or 5°C) for up to 14 d. The effect of winter severity on survivorship was then evaluated by exposing fish to simulated cold-front events of varying frequency and duration. Body size was incorporated as a factor into each set of experiments. Age 0 red drum were intolerant of even brief exposure to temperatures ≤3°C and experienced mortality after prolonged exposure to 5°C. Higher frequency of simulated cold-front events impacted survivorship more than longer-event duration, and recovery time between events improved survivorship. Size-dependent mortality was only evident for fish exposed to mild and moderate winter severity conditions, with larger fish surviving longer. For juvenile red drum, severe winters may cause high mortality independent of body size, whereas size-dependent year-class restructuring may occur during milder winters.

Keywords: acute cold stress, overwinter mortality, red drum, size-selectivity, winter severity.

Introduction

Overwinter mortality can represent an important process that shapes the population dynamics of fish at temperate latitudes, especially during early life. The association between autumn and spring abundance can often be disrupted during winter, an indication that year-class strength may not be established until after the first winter of life (Hurst and Conover, 1998; Michaletz, 2010). Many studies have noted decreased food availability in winter causing fish to exhaust energy reserves and starve (reviewed in Hurst, 2007). However, at extreme cold temperatures, the depletion of energy stores may no longer determine survival; rather, acute thermal stress can disrupt osmoregulatory function and be the primary cause of death (Hochachka, 1988; Belkovskiy *et al.*, 1991; Johnson and Evans, 1996; McCollum *et al.*, 2003). Exposure to extended periods of extreme cold and the associated acute thermal stress may, in fact, account for much of the observed overwinter mortality for several important US Mid-Atlantic fish stocks (Malloy and Targett, 1991; Hurst and Conover, 1998; Lankford and Targett, 2001).

Winter mortality has often been found to be size-dependent, with the potential for lasting influences on cohort demographics. Small fish are generally hypothesized to be more vulnerable to overwinter starvation due to their higher relative energetic demands coupled with a reduced capacity for lipid storage (Post and Evans, 1989). In addition, smaller individuals may also be more susceptible to osmotic failure caused by acute thermal stress due to a larger ratio of gill surface area to body mass (Hughes, 1984). Several field (Hunt, 1969; Post *et al.*, 1998;

Michaletz, 2010) and laboratory (Post and Evans, 1989; Johnson and Evans, 1991; Pangle *et al.*, 2004) studies have provided evidence for size-selective winter mortality that removes a greater fraction of small individuals. Alternatively, in some cases, small fish have been noted to experience greater relative survival when exposed to extreme cold temperatures, possibly related to improved acclimation as a result of faster protein turnover in small fish (Lankford and Targett, 2001; Slater *et al.*, 2007). Mortality during winter may also be size-independent (Cnaani *et al.*, 2000; McCollum *et al.*, 2003). Finally, even under identical winter conditions, size-selective mortality may be a dominant process for some species, but not for others (Toneys and Coble, 1979; Hales and Able, 2001).

Both the intensity of size selection and the overall magnitude of overwinter mortality can vary interannually. For size-selective mortality to occur, sufficient intracohort contrast in body size must exist and be coupled with high and non-random mortality (Sogard, 1997). If prewinter body sizes are relatively large on average, the disproportionate mortality of small fish may be unobservable or weak in given years due to fewer individuals being small enough to be susceptible to winter stress (Hurst and Conover, 1998). However, if juvenile growth rates during autumn are density-dependent, numerically large year classes may result in many small individuals that are more susceptible to cold-related sources of mortality at the onset of winter (Ludsin and DeVries, 1997). In contrast, during severe winters, high rates of mortality can negatively impact an entire cohort regardless of body size (McCollum *et al.*, 2003; Michaletz, 2010). Therefore, it is plausible that density-dependent processes will have a greater impact on overwinter survival during mild or moderate winters. The strength of size selectivity can also vary across a latitudinal gradient. Empirical evidence supports the notion that size-dependent overwinter mortality caused by acute cold stress should be less common at the extremes of a species' geographic range since threshold temperatures may affect all fish equally (Michaletz, 2010), whereas others have demonstrated strong size selection caused by starvation at the edges of a species' distribution, especially at northern range limits (Post *et al.*, 1998). Ultimately, the existence and strength of size-dependent mortality during winter may be influenced by various factors, including cohort demographics and winter severity (Shuter and Post, 1990).

The red drum (*Sciaenops ocellatus*) is a temperate marine fish that experiences variable winter conditions throughout its range in the US South Atlantic and Gulf of Mexico. The species is highly prized as a sportfish, and recent management efforts have promoted recovering stocks (SEDAR, 2009). Adults spawn in coastal waters during late summer and autumn (Ross *et al.*, 1995; Stewart and Scharf, 2008); offspring are then transported to estuarine habitats. Early juveniles are demersal and experience variable growth during autumn (Rooker *et al.*, 1999). Juvenile and subadult red drum generally occupy estuarine habitats for 3–4 years before joining the mature adult segment of the stock in mostly nearshore oceanic habitats (Ross *et al.*, 1995).

Evidence from both long-term surveys and focused studies indicates that overwinter mortality could have a considerable impact on red drum fishery recruitment. Scharf (2000) identified a clear lack of association between age 0 and 1 abundance indices collected over 20+ years along the Texas coast. Similarly, an abundance index for juvenile red drum estimated annually since 1991 in North Carolina waters showed only modest correlation with subsequent fishery landings data, with a substantial amount of unexplained variation (Bacheler *et al.*, 2008). Field-based estimates of age 0 red drum overwinter loss (mortality plus any potential emigration) from a North Carolina estuary have ranged between 35 and 90% (Stewart and Scharf, 2008; Martin, 2009). The spawning period for red drum is relatively protracted (Comyns *et al.*, 1989; Stewart and Scharf, 2008; Martin, 2009), which generates up to threefold variation in body sizes before winter (Martin, 2009). An examination of pre- and post-winter cohort demographics in North Carolina revealed evidence of selective overwinter mortality, with both early-hatched and fast-growing individuals realizing higher survivorship (Martin, 2009). Intracohort variability in survivorship was also observed for recently settled red drum in a Texas estuary (Rooker *et al.*, 1999).

Given the potential contribution of first-year processes in determining the year-class strength of red drum, a more comprehensive understanding of the patterns and mechanisms of overwinter mortality is warranted. Here, we report on the outcome of a series of controlled laboratory experiments devised to determine the size-dependent response of first-year juvenile red drum to variable winter conditions. The objectives of our experiments were to: (i) estimate the survival patterns of juvenile red drum exposed to different thermal minima; (ii) evaluate the influence of winter severity, indexed using the duration and frequency of cold-front events, on juvenile red drum survivorship; and (iii) test for size-selective mortality patterns across a range of winter conditions. Experiments were designed specifically to assess the potential effects of acute cold stress associated with exposure to extreme cold temperatures, rather than longer-term effects related to starvation.

Material and methods

Fish collection and experimental setup

Age 0 red drum were collected during autumn 2010 and 2011 in the New River estuary, NC, USA. Sites identified as juvenile red drum habitats during prior research (Stewart and Scharf, 2008) were accessed by boat and sampled using a 30.5 × 2.0-m beach-seine (6.0 and 3.0 mm stretched mesh in the wings and bag, respectively). At each site, dissolved oxygen ($\mathrm{mg\,l^{-1}}$), salinity (psu), and temperature (°C) were recorded using an YSI Model 85 multiprobe. Juvenile red drum (~30–60 mm total length (*TL*)) were removed from the catch and transported to the laboratory in aerated containers (140 l). Fish were transferred to holding tanks (900 l) that were part of a recirculating system maintained at ambient autumn water temperatures (~15°C) and moderate salinities (~17 psu). Juvenile red drum were fed to satiation once daily with a combination of larval fish feed (Marubeni Nisshin Feed Co., Ltd, Tokyo, Japan) and thawed adult *Artemia*. Although laboratory conditions may have promoted faster growth relative to field conditions, we attempted to regulate growth during holding and acclimation by maintaining cool water temperatures and feeding fish only a maintenance ration ($\leq$5% mass $\mathrm{d^{-1}}$). Holding tanks were monitored daily for dissolved oxygen, salinity, and temperature and were maintained on a 10/14-h light/dark photoperiod to simulate natural light conditions in coastal waters of the US Mid-Atlantic during winter. Any dead individuals were removed daily and counted. Fish were acclimated to laboratory holding tanks for a minimum of 4 weeks before the start of an experiment.

Controlled experiments were conducted during two consecutive winters (2010/2011 and 2011/2012) using circular, polyethylene tanks (94 l), which were housed in an environmentally controlled chamber. Air temperature in the chamber was set below the minimum water temperature of any of the experimental treatments, and water in individual tanks was heated to specific treatment temperatures using titanium heaters (1000 W; Process Technology, Mentor, OH, USA) and digital temperature controllers with ±1.0°C accuracy. Water quality in each tank was maintained with a power filter (AquaClear 30, Hagen Corp., Montreal, Canada) that provided mechanical and biological filtration. A temperature data logger (HOBO Pro v2, Onset Computer Corporation, Boston, MA, USA) was tethered underwater in each tank and programmed to record hourly water temperature. Salinities were maintained at mid-estuary levels of 18–23 psu, and the chamber was programmed for a 10/14-h light/dark photoperiod. Between each replicate run, filters were cleaned, a new carbon pack installed, and an 80% water change was performed.

Past water temperature data collected during winter (1 December–1 March) by the US Geological Survey (USGS) National Water Information System was analysed to identify typical and extreme winter weather patterns along the North Carolina coast. Specifically, we examined data collected from 2007 to 2011 in the New River estuary at Jacksonville, NC (USGS site 0209303205), and from 1999 to 2009 in the Pamlico River estuary at Washington, NC (USGS site 02084472). These data were used to determine the average winter water temperatures and thermal minima occurring in North Carolina coastal waters occupied by juvenile red drum. Minimum daily temperatures during winter at the New River estuary site ranged from 1.6 to 6.7°C, whereas daily minima in the Pamlico River estuary ranged from 0.4 to 5.2°C. We also examined historical fluctuations in the minimum water temperature along the North Carolina coast during winter to define mild and severe winters based on the frequency and the duration of extreme cold events associated with the passage of fronts (hereafter referred to as cold-front events). These natural cold-front events can be described generally as a rapid decrease in temperature, followed by a brief period holding at a minimum temperature, then a gradual increase in temperature. Typical natural cold-front events exhibited a water temperature decrease of ≥2°C in 24 h or ≥3°C in 36 h. For each event, we calculated the rate of temperature decline and recovery, along with the time spent at the minimum temperature. Combining cold-front data from both of the estuaries with historical water temperature data, the average rate of decline over 24 h was 2.34°C, with a maximum temperature drop of 4.8°C in 24 h. The vast majority of these events included 1–4 consecutive days at a minimum temperature, with roughly between 0 and 10 separate events each winter. Therefore, the historical water temperature data provided a framework that was used to identify appropriate temperature treatments within each set of experiments.

Thermal-tolerance experiments

During winter 2010/2011, experiments were designed to determine the thermal tolerance of juvenile red drum exposed to different minimum water temperatures. Treatment levels included water temperatures of 1, 3, and 5°C, selected based on the observed minimum temperatures during winter in North Carolina estuaries. Although 1 and 3°C occur less frequently than 5°C in North Carolina estuaries, juvenile red drum overwintering in these estuarine habitats can be exposed to temperatures as low as 1°C during severe winters. A control treatment level of 10°C was selected to mimic the average winter estuarine temperatures. To test for the effect of body size, fish were separated into large (grand mean ± s.d. = 90.98 ± 12.51 mm *TL*, 7.05 ± 2.72 g wet weight) and small (72.58 ± 12.89 mm *TL*, 3.85 ± 1.93 g wet weight) groups, which differed significantly in body size, both overall (*TL*: $F = 187.5$, $p < 0.001$; weight: $F = 164.2$, $p < 0.001$) and within each trial (all $p < 0.001$ for both *TL* and weight comparisons). Each trial consisted of eight tanks (2 body size treatment levels × 4 temperature treatment levels), with each tank containing 15 individuals. The experimental response was proportional survival and was measured for each replicate tank. The use of 15 individuals within each tank provided an adequate level of precision to measure the response of each replicate. Each experimental trial lasted ~3 weeks, and three trials were completed between 11 January and 26 March 2011. Within small- and large-size groups, body sizes were not significantly different among treatments within each trial (small: all $p \geq 0.622$ for *TL* and ≥ 0.805 for weight; large: all $p \geq 0.833$ for *TL* and ≥ 0.775 for weight). While body sizes of both size groups were larger in subsequent trials due to fish growth in the holding tanks, significant levels of contrast (at least 15.20 mm *TL* and 2.66 g difference between small and large groups) were maintained between size groups during each replicate trial.

To initiate each experimental trial, fish were measured for *TL* (mm) and wet weight (g) as they were transferred from holding tanks to the experimental tanks in the environmental chamber. Fish were acclimated to 10°C water temperatures for at least 48 h before each trial. For non-control tanks, water temperature was then decreased by $1^{\circ}\mathrm{C\ d}^{-1}$ until the specified treatment level temperature was reached. For observational purposes, day 1 of each trial was defined as the day when all non-control tanks reached 5°C. Each trial then continued for 14 d. For 3 and 1°C treatment levels, water temperature was decreased by 1°C each day thereafter until the specified temperature was reached. Observations were completed three times a day at ~08:00, 12:00, and 16:00. During each observation, fish behaviour and any mortality were recorded, along with water temperature and salinity. Fish were fed to satiation with adult *Artemia* during the midday observation, and feeding behaviours were documented. Mortality was defined using two factors: no response to stimulus and no opercular movement (Lankford and Targett, 2001). Dead fish were removed with a dipnet, and the observation time was assigned as time of death. Weight and *TL* were recorded for each dead fish.

Cold-front-event simulations

During winter 2011/2012, experiments were designed to determine the effects of exposure to variable winter severity, characterized by the frequency and the duration of cold-front events, on juvenile red drum survivorship. Given the historical variability that we identified in both the number (0–10 events per winter) and the duration (1–4 d at minimum temperatures) of cold-front events, we elected to index winter severity based on these two traits.

First, we defined a simulated cold-front event as a decrease from 8 to 3°C over 36 h, exposure to a 3°C minimum for a specified duration (see below), followed by a temperature recovery to 8°C over 48 h. A 5°C drop over 36 h was slightly more rapid than the average decrease observed in the historical estuary temperature data, but it was conservative relative to the observed maximum declines of over 4°C in 24 h. Although minimum temperatures associated with cold-front events varied to some degree within the historical data, we chose 3°C as the minimum temperature reached during each simulated event based on the results from our thermal-tolerance experiments. Juvenile red drum survived at 3°C, but acute cold stress was apparent, and fish began to experience mortality within a short time after exposure. We varied the frequency of cold-front events by exposing fish to either three consecutive events or two events separated by a recovery period at 8°C the same length as a cold-front event. Duration, or the total time spent at the minimum temperature, was set at either 24 or 48 h. Each frequency (high = 3, low = 2) was crossed with each duration (long = 48 h, short = 24 h) to create four distinct winter severity treatment levels (Figure 1). The most severe winter conditions consisted of three consecutive cold-front events, each including 48 h at the minimum temperature, whereas mild winter conditions were simulated by exposure to two cold-front events each including only 24 h at the minimum temperature, separated by a recovery period. The other two treatment levels were deemed to represent intermediate winter conditions. Each winter severity treatment level was tested for two body size groups, resulting in eight replicate tanks (4 winter severity treatment levels × 2 body size groups) for each of three trials, which were run consecutively from 25 January to 7 April 2012. Fish were assigned to either a large (73.97 ± 7.72 mm TL, 3.66 ± 1.33 g wet weight) or a small (52.29 ± 5.17 mm TL, 1.32 ± 0.38 g wet weight) body size group, which were statistically distinct both overall (TL: $F = 1046$, $p < 0.001$; weight: $F = 544.2$, $p < 0.001$) and within each trial (all $p < 0.001$ for both TL and weight). Individual tanks contained 16 juvenile red drum to achieve sufficient precision in survival estimates; however, any individuals that died during the acclimation period were removed from the experiment and not replaced.

Fish were weighed and measured before being randomly assigned to experimental tanks. All fish were then held at 8°C for a 48-h acclimation period. All tanks within each trial were exposed to the first cold-front event beginning on day 1. Since each short-duration, cold-front event lasted 5 d, trials consisting of short-duration events (either three cold-front events or two cold-front events, separated by a recovery period) lasted 15 d. Similarly, each long-duration, cold-front event lasted 6 d, so trials lasted 18 d to complete all events. Observations were made when treatments required temperature adjustments, which occurred every 9 h during temperature decrease and every 12 h during temperature recovery. While fish were held at the minimum temperature, observations were made every 12 h. Fish behaviour and any mortalities, as well as water temperature and salinity, were recorded. Fish were fed to satiation at the earliest observation time each day. Similar to the thermal-tolerance experiments, growth occurred in the holding tanks across trials, but significant levels of contrast in body size were maintained (at least 20.89 mm TL and 2.19 g weight difference between small and large groups). Similar to thermal-tolerance experiments, no significant differences existed within small or large body size groups in any of the trials (small: all $p \geq 0.416$ for TL and ≥ 0.654 for weight; large: all $p \geq 0.763$ for TL and ≥ 0.787 for weight).

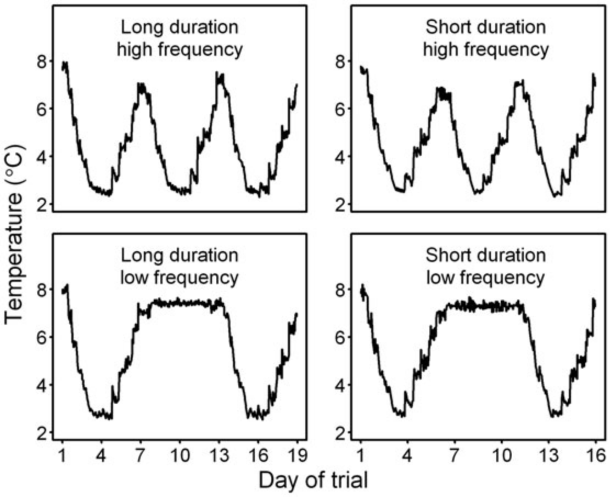

Figure 1. Experimental design for cold-front-event simulations. Four levels of winter severity were simulated by varying the duration held at the 3°C minimum water temperature (long = 48 h, short = 24 h) and the frequency of events (high = 3, low = 2). The total time for trials including long-duration events was slightly longer (by 3 d) and is represented in the scale of the x-axes.

Data analysis

To assess fish condition after exposure to experimental treatments, Fulton's condition factor ($K = \text{weight}/\text{length}^3 \times 10^5$) was calculated for each individual then averaged for each replicate tank. The condition factor was estimated for each fish both at the start and at the end of each trial, or upon death. For both sets of winter experiments, the initial condition did not differ among treatments (thermal tolerance: $F = 0.249$, $p = 0.862$; cold-front-event simulation: $F = 0.822$, $p = 0.482$). Fish in the small body size groups had higher initial condition than those in the large body size groups (thermal tolerance: $F = 20.129$, $p < 0.001$; cold-front-event simulations: $F = 14.337$, $p < 0.001$); this was expected based on growth allometries (Froese, 2006). No significant interaction between treatment and body size was detected in either winter. The final condition was assessed by comparing the relative change in the condition factor ($\Delta K = \text{initial } K - \text{final } K$) among treatments and body sizes during each winter using a two-way analysis of variance (ANOVA).

The effects of our experimental treatments on juvenile red drum survivorship were also analysed using two-way ANOVA models in which we considered both body size and temperature treatment as fixed effects. Since some thermal minima treatments of the first winter resulted in no survivors, the analysis was conducted using median survival time (median lethal time = LT_{50}) per replicate tank as the response variable. For the cold-front-event simulation experiments, proportional survivorship per tank at the end of each trial was analysed as the response variable, after first applying a logit transformation (Warton and Hui, 2011). Any *post hoc* multiple comparisons were conducted using Tukey's honestly significant difference (HSD) test with an experiment-wise error rate of 0.05.

Survival analysis was used to examine the effects of our experimental treatments on patterns of mortality at a finer temporal scale. In this study, the response variable was time until death, our event of interest. We also incorporated right-censored data (i.e. individuals that did not experience death) into our survival analysis, since survivors remained in several trials. Additionally, a subset of fish was sacrificed for physiological analysis of tissue samples to assess potential osmoregulatory disruptions related to acute cold stress as part of a separate study. Fish that were sacrificed during thermal-tolerance experiments were not censored, since they exhibited moribund behaviours indicating imminent mortality. However, during the cold-front-event simulations, apparently healthy fish were sacrificed at set times due to the complex nature of the temperature regimes. These fish did not display the obvious signs of death before being sacrificed, thus they were censored in our analysis.

For our survival analysis, the Kaplan–Meier survival curves were first generated to graphically illustrate general survival patterns (Kaplan and Meier, 1958). To further compare survival patterns among temperature treatments and body sizes, the semi-parametric Cox proportional hazards model was applied to the data (Cox, 1972). Since fish were grouped in tanks to which the treatment was applied, responses of individual fish may not have been independent. This could be due to behavioural interactions or unmeasured random effects within tanks. To test for clustering in responses due to lack of independence, a shared gamma frailty model was used (Rondeau *et al.*, 2003). The hazard function for the shared frailty model is expressed as:

$$\lambda_{ij}(t|\nu_i) = \nu_i\lambda_0(t)\exp(\beta_i X_{ij}) = \nu_i\lambda_{ij}(t), \tag{1}$$

with the baseline function $\lambda_0(t)$, the covariate X_{ij} associated with regression coefficient β, and the random effect ν_i for the ith group, which were individual tanks in our case (see Rondeau *et al.* (2012) for additional details on shared frailty models). Model parameters were estimated based on a maximization of the penalized likelihood using frailtypack in R (R Development Core Team, 2012; Rondeau *et al.*, 2012). The presence of heterogeneity among subjects located within a given tank was determined using a modified Wald test of the variance for the frailty term (Rondeau *et al.*, 2012). After initial testing, we concluded that there were no significant random effects within tanks. Therefore, the frailty term ν_i could be excluded from the model, which then simplified to a basic Cox proportional hazards model, where the hazard function is expressed as:

$$\lambda_j(t) = \lambda_0(t)\exp(\beta_j X_j), \tag{2}$$

which was also estimated using a penalized likelihood approach in R. Although we deemed that a frailty parameter was not necessary, tanks were still analysed as clustered groups to account for a potential lack of independence among individual fish. The Cox model was then applied to determine both treatment and body size effects. To distinguish the effects of winter severity conditions, body sizes were combined in the Cox model. The effect of body size on survival patterns was determined using pairwise comparisons of large- and small-size groups within each treatment level. A significance level of $\alpha = 0.05$ was used for all tests.

Results

Behavioural observations and fish condition

At water temperatures below 5°C, juvenile red drum exhibited reduced affinity for food, with limited observations of actual foraging when prey was offered. Fish activity, aside from lack of feeding, was also reduced by extreme cold temperatures. Generally, fish were stationary at water temperatures below 5°C and often rested at the bottom of the tank displaying very little movement. During simulated cold-front events in which fish were held for specified durations at 3°C, normal behaviour resumed once water temperature recovered to ~7°C.

The average change in fish condition (mean ΔK) for 10, 5, 3, and 1°C treatments during cold-tolerance experiments with body sizes combined was 0.070, 0.074, 0.062, and 0.057, respectively, with no significant effects of temperature treatment, body size, or their interaction (two-way ANOVA, all $p \geq 0.242$; Figure 2). During cold-front-event simulations, with body sizes combined, the mean ΔK was 0.095, 0.081, 0.063, and 0.035 for short/low, long/low, short/high, and long/high winter severity treatments, respectively. Similarly, no significant effect of winter severity treatment, body size, or their interaction was detected (two-way ANOVA, all $p \geq 0.141$; Figure 2).

Thermal-tolerance experiments

Thermal-minima treatment levels of 1 and 3°C resulted in 0% survivorship for age 0 red drum, whereas fish held at 5°C realized mean ± s.d. survivorship of 20.0 ± 4.2%, and we observed no mortality for control fish held at 10°C (Table 1). No significant interactive effect of temperature treatment and body size on median lethal time was detected ($F = 0.139$, $p = 0.872$; Table 3), which enabled clear interpretation of the main effects. For the 1, 3, and 5°C treatment levels, the median lethal times were 5.17, 6.25, and 11.33 d, respectively, which were significantly different (ANOVA; $F = 18.228$, $p < 0.001$; Table 3; Figure 3a). *Post hoc* comparisons revealed that the median survival time for fish held at 5°C was significantly greater than that held at 1°C ($p < 0.001$) and 3°C ($p = 0.002$), which were not different from each other. The time-specific patterns of mortality varied considerably among the thermal minima (Figure 4a). It is noteworthy that fish in the 1°C treatment did not reach the minimum temperature until day 5, with a mean ± s.d. survivorship of only 28.9 ± 4.8% at the point when 1°C was attained. Within 24 h of reaching 1°C, no survivors remained in any of the trials for this treatment level. Fish in the 3°C treatment experienced more gradual mortality, with survivorship declining to zero within 6 d after arriving at the minimum temperature on day 3. Survivorship in the 5°C treatments remained above 90% for ~6 d, after which mortality increased steadily for the remainder of each trial.

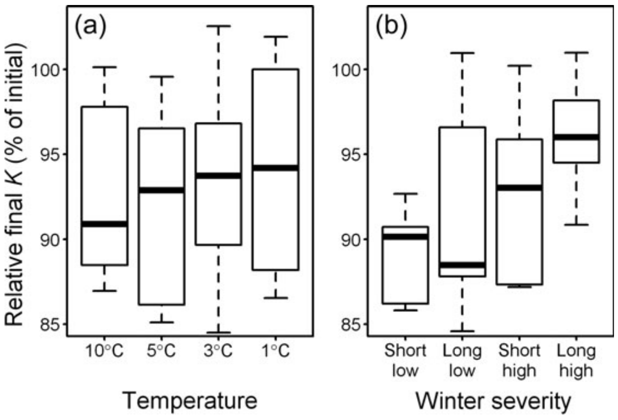

Figure 2. Box and whisker plots of relative final condition factor (final K/initial $K \times 100\%$) for (a) thermal-tolerance experiments and (b) cold-front-event simulations. For interpretation, a fish maintaining its initial condition ($\Delta K = 0$) would have a relative final condition factor of 100%. Thick line within each box = median. Whiskers extend to maximum and minimum values. Statistical differences do not exist among treatment groups within each winter, as determined by Tukey's HSD test ($\alpha = 0.05$).

Table 1. Numbers of fish and mean *TL* (mm) used in thermal-tolerance and cold-front-event simulation experiments, along with survivorship results

	Thermal-tolerance experiments				Cold-front-event simulations			
Treatment level	**1°C**	**3°C**	**5°C**	**10°C**	**Long/high**	**Short/high**	**Long/low**	**Short/low**
n	90	88	90	88	82	84	83	84
Small body size	72.1	72.6	73.0	72.6	51.9	52.1	52.3	52.9
Large body size	92.0	90.1	90.9	90.9	73.7	73.8	74.0	74.5
Small survival (%)	0	0	26.7	100	21.7	39.4	50.6	55
Large survival (%)	0	0	13.3	100	12.6	71.9	85	97.6
Overall survival (%)	0	0	20	100	17	55.8	68.3	76.4

During each set of experiments, replicate trials consisted of eight tanks (4 temperature treatments × 2 body sizes) with 13–16 juvenile red drum per tank. Survivorship results are means for three replicate trials.

Table 2. Parameter estimates generated from fitting Cox proportional hazards models.

Treatment level	β	exp(β)	s.e.(β)	*p-value*
10°C	−12.159	$5.241e^{-6}$	9.154	0.184
3°C	2.403	11.054	0.244	<0.001
1°C	3.952	52.030	0.288	<0.001
Long/low	−0.014	0.986	0.293	0.962
Short/high	0.925	2.523	0.276	<0.001
Long/high	1.562	4.770	0.251	<0.001

The response of each of the thermal-tolerance treatment levels is relative to the 5°C treatment level response. Cold-front-event simulation effects are relative to the treatment level simulating the mildest winter severity (short duration/low frequency). Hazard ratios are expressed by exp(β).

Table 3. ANOVA results for thermal-tolerance and cold-front-event simulation experiments including body size as a factor.

Factor	Sum of squares	d.f.	Mean square	*F*	*p*-value
Thermal-tolerance experiments					
Temperature	122.365	2	61.182	18.228	<0.001
Body size	0.038	1	0.0383	0.011	0.917
Temperature × size	0.932	2	0.466	0.139	0.872
Residual	40.279	12	3.357		
Cold-front-event simulations					
Winter severity	30.312	3	10.104	5.240	0.010
Body size	10.446	1	10.446	5.417	0.033
Severity × size	7.030	3	2.343	1.215	0.336
Residual	30.854	16	1.928		

The response for thermal-tolerance experiments was median survival time (LT_{50}). For cold-front-event simulations, the response was logit-transformed final survivorship.

The Cox analysis predicted the effects of different minimum temperatures relative to the model for the mildest treatment level (thermal minimum = 5°C). Temperatures of 1 and 3°C both had a highly significant effect on survival ($p < 0.001$ for both; Table 2) relative to the 5°C group. The hazard ratio indicated that individuals held at 3°C were more than 11-fold likely to experience mortality than those held at 5°C. Likewise, fish held at 1°C were more than 52-fold likely to die than those held at 5°C. The relative risk was non-existent (the hazard ratio was not significant) for control fish held at 10°C.

Size-dependent mortality was not evident during thermal-tolerance experiments (Table 3; Figure 3a). Although the temperature treatment significantly affected LT_{50}, the effect of body size was not significant ($F = 0.011$, $p = 0.917$). Similarly, hazard ratios did not differ significantly between large- and small-size groups within any of the temperature treatment levels (Table 4).

Cold-front-event simulations

Fish subjected to the mildest winter conditions, indexed by short-duration, cold-front events occurring at low frequency, experienced the highest mean survivorship (Table 1). Both the long-duration/low-frequency and the short-duration/high-frequency treatment levels produced intermediate survivorship, whereas the treatment level simulating the most severe winter conditions, long-duration/high-frequency, resulted in the lowest survivorship. Similar to thermal-tolerance experiments, no significant interactive effects of winter severity treatment and body size were detected ($F = 1.215$, $p = 0.336$; Table 3), which enabled a clear interpretation of the main effects. Final survivorship was significantly different ($F = 5.240$, $p = 0.010$; Table 3; Figure 3b) among winter severity treatment levels. The survivorship of fish exposed to the most severe winter conditions (long-duration/high-frequency) was significantly lower than for fish exposed to the low-frequency treatments, both short- ($p = 0.009$) and long-duration events ($p = 0.035$), but was not statistically different from the survivorship of fish exposed to the high-frequency/short-duration treatment. Although the overall timing of mortality varied across winter conditions, temporal patterns were similar (Figure 4b). In each case, fish generally survived the first cold-front event well, with >90% survivorship for all treatment levels at the end of the first cold-front event. Fish subjected to either of the low-frequency treatment levels maintained survival above 90% through the non-front-recovery period, then experienced greater mortality during the second cold-front event. Mortality increased successively for fish subjected to each of the high-frequency treatment levels during the second and third cold-front events. Survivorship decreased by ~10% during the 24-h event duration when fish were held at 3°C, while longer-duration (48 h) events resulted in ~20% lower survivorship during the frontal period. Fish subjected to each level of winter severity experienced some delayed mortality following the passage of a simulated cold front, with greater delayed mortality for fish exposed to the most severe winter conditions.

Survivorship, when exposed to the mildest winter conditions (short-duration/low-frequency), was used to determine relative risk when we estimated the Cox proportional hazards model. Exposure to the long-duration/low-frequency treatment level did not significantly affect the relative survival of fish ($p = 0.962$,

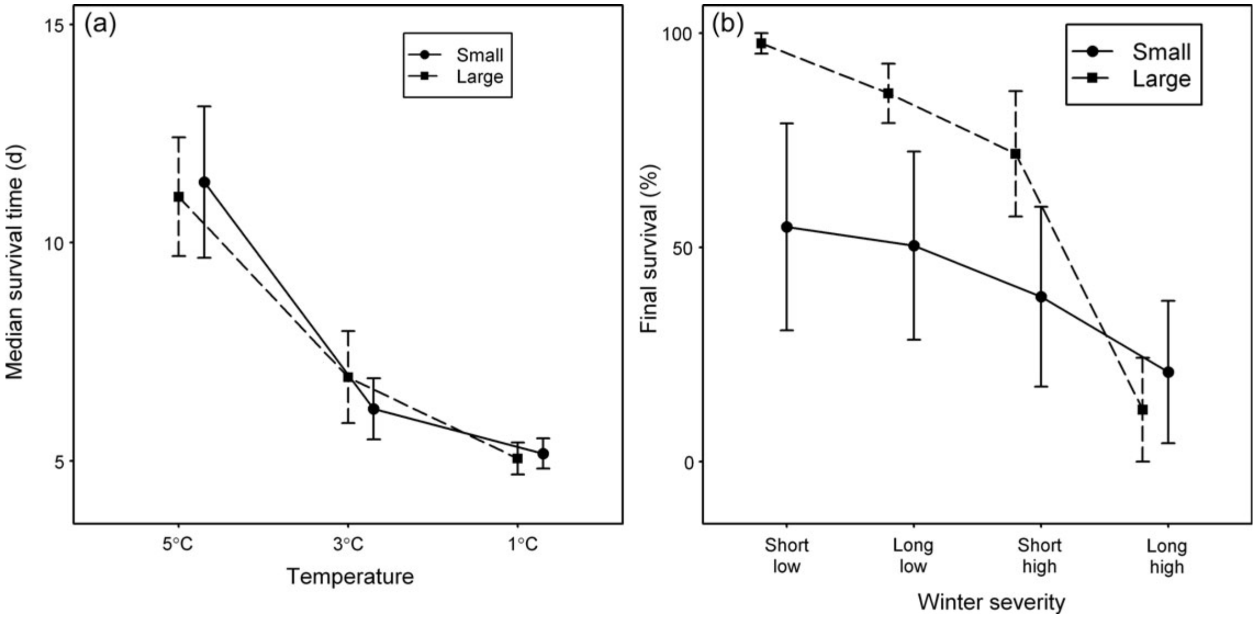

Figure 3. Survivorship results for thermal-tolerance experiments (a) and cold-front-event simulations (b). (a) The median survival time (LT_{50}) by the body size group for 1, 3, and 5°C treatment levels. (b) The final survivorship (%) by the body size group in each of the four winter severity simulations. Responses (median survival time or final survivorship) were averaged across replicate trials. Body size is distinguished as small (black circle) or large (black square). Error bars = 1 s.e., calculated by dividing s.d. by $\sqrt{3}$, where 3 = number of replicate tanks. In each panel, symbols are offset slightly for clarity.

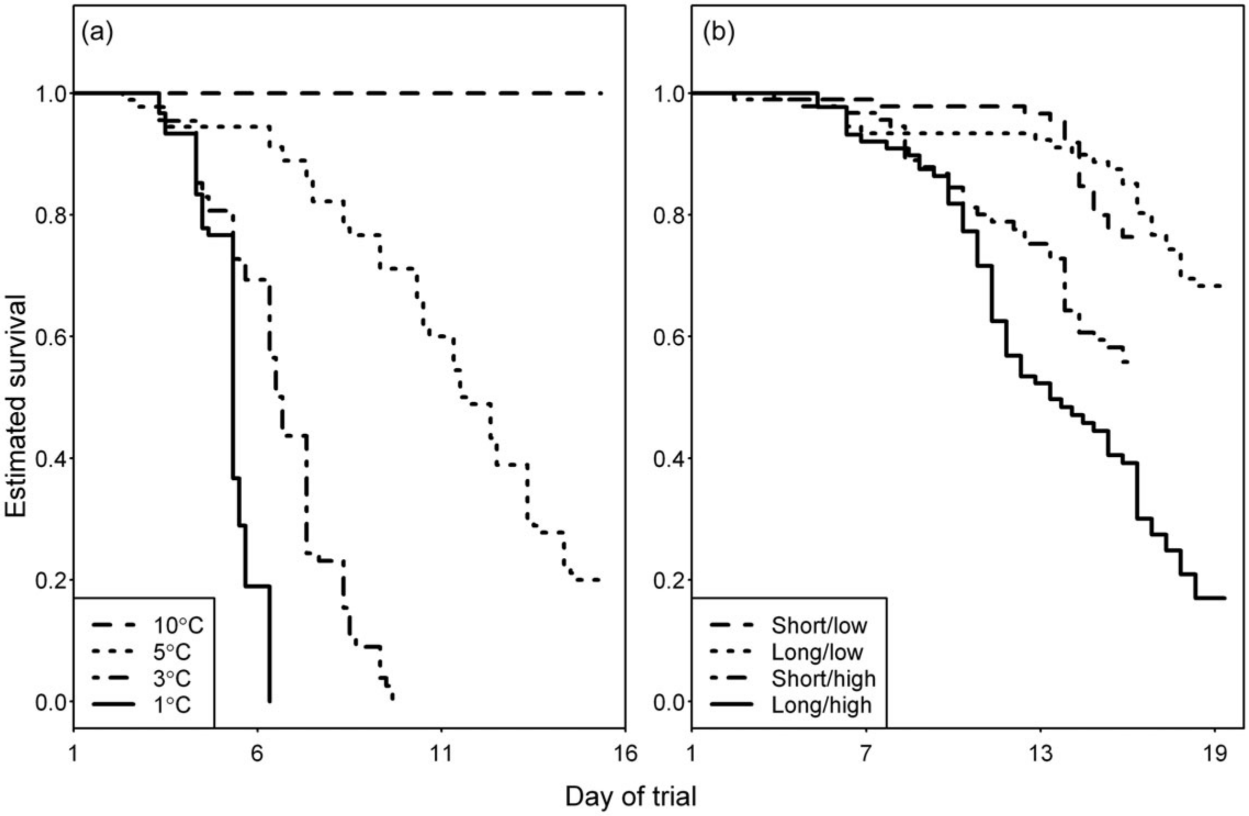

Figure 4. The Kaplan–Meier survival curves for (a) thermal-tolerance experiments and (b) cold-front-event simulations. Treatment levels that ended with survivors were right-censored in the analysis.

Table 4. Cox proportional hazard ratios expressed as exp(β) for small fish relative to large fish during thermal-tolerance experiments and cold-front-event simulations.

Temperature/winter severity	exp(β)	*p*-value
1°C	0.934	0.752
3°C	1.437	0.109
5°C	0.736	0.198
Short/low	27.200	$<$0.001
Long/low	3.938	0.003
Short/high	3.353	$<$0.001
Long/high	1.036	0.883

Table 2). However, fish subjected to both high-frequency treatment levels experienced greater mortality risk relative to simulated winters with a low frequency of cold-front events. The relative risk of mortality was 2.52-fold ($p < 0.001$) and 4.77-fold ($p < 0.001$) greater for fish subjected to the short-duration/high-frequency and long-duration/high-frequency treatment levels, respectively.

Mortality was dependent on body size when fish were exposed to varying levels of winter severity indexed by the duration and the frequency of cold-front events (Table 3; Figure 3b). The final survivorship was significantly ($F = 5.417, p = 0.033$) affected by body size. Hazard ratios also differed between large and small body sizes in three of the four winter severity treatment levels (Table 4). When subjected to the mildest winter conditions, small fish had a risk of mortality 27.2-fold greater than large fish. Smaller fish also experienced greater relative mortality risk (~three–fourfold greater risk, depending on the treatment level) than large fish when exposed to moderate winter conditions. In contrast, no difference in the hazard ratio between small and large fish was observed for fish exposed to the most severe winter conditions.

Discussion

Impact of variable winter severity on survival

Juvenile red drum exposed to water temperatures ≤5°C experienced mortality caused by acute cold stress. Specifically, exposure to thermal extremes ≤3°C resulted in rapid death. As water temperatures were reduced (at a rate of 1°C d^{-1}), we noted considerable declines in survivorship (e.g. ~40% mortality at 2°C) before reaching temperature minima, which resulted in only a small portion (~30%) of individuals remaining alive to experience our most extreme thermal challenge (1°C minimum temperature). Furthermore, within 4 h of exposure to 1°C water temperatures, an additional 10% of the fish expired, and no survivors remained after 16 h. Our findings are similar to previous studies reporting on the limits to low-temperature tolerance for red drum. Procarione and King (1993) found that 50% mortality was reached at water temperatures between 2.6 and 3.5°C for both Texas and South Carolina juvenile red drum acclimated to 14 or 16°C conditions. Their findings also provided evidence that acclimation temperature before exposure to extreme cold affected survivorship, with fish acclimated to cold conditions performing better. Miranda and Sonski (1985) reported a similar susceptibility of juvenile red drum to cold temperatures and also observed a modest effect of acclimation temperature on survivorship. Minimum water temperatures causing 50% mortality in their study were 1.9 and 2.4°C for fish acclimated to 15 and 25°C, respectively. Our findings related to fish condition after exposure to the experimental treatments support acute cold stress, rather than nutritional deficiency, as the proximate cause of death. Exposure to winter conditions, both mild and severe, resulted in a decrease in final *K* relative to initial *K*, most likely attributable to decreased feeding rates at cold temperatures. However, the average change in the condition factor (ΔK) did not differ among temperature treatments or body sizes. In fact, we noted a trend for larger decreases in *K* for fish exposed to milder temperature treatments, which we attributed simply to those fish being exposed to winter conditions, and thus reduced feeding rates, for a longer period. Alternatively, mortality occurred much earlier for fish exposed to more extreme temperature treatments, with less time for reduced feeding rates to impact fish condition.

Our results confirm the likely importance of episodic cold events in causing mortality of red drum during juvenile life stages. Indeed, mass mortality events for coastal fish, including red drum, have occurred with some regularity along the Texas coast (Gunter, 1941; McEachron *et al.*, 1994). Previous laboratory results (Miranda and Sonski, 1985; Procarione and King, 1993) indicate that acclimation to colder conditions can buffer the impacts of episodic cold events, implying that red drum acclimated to winter conditions in North Carolina may be more resistant to extreme and rapid declines in water temperature. Winter fish kills have historically been rare in North Carolina coastal waters (see annual reports compiled by the NC Department of Natural Resources; http://portal.ncdenr.org/web/wq/ess/fishkillsmain), with reports of red drum mortality during these events being infrequent. However, cold temperatures that have been found to be lethal to red drum occur much more regularly in North Carolina coastal systems than along the northern Gulf of Mexico coast. Prolonged exposure to extreme cold temperatures is likely to result in the mortality of red drum, regardless of acclimatization, as has been observed for other species (Hurst and Conover, 1998; McCollum *et al.*, 2003; Fetzer *et al.*, 2011). We observed higher survivorship for juvenile red drum held at 5°C, relative to 1–3°C temperatures, but total survival after 14 d exposure was still only 20%, and half of the fish had died by ~11 d. Therefore, even exposure to less extreme winter water temperatures may result in high levels of mortality for juvenile red drum if the exposure is prolonged.

Juvenile red drum were able to tolerate exposure to water temperatures as low as 3°C for brief periods, as evidenced by the results from experiments simulating the occurrence of cold-front events. Initial survivorship was relatively higher when fish were faced with abrupt, but short, exposure to stressful temperatures compared with continuous, prolonged exposure during thermal-tolerance experiments. Mortality reached 18 and 29% after exposure to 3°C for 24 and 48 h, respectively, during thermal-tolerance experiments. In contrast, all four winter severity treatment levels in our cold-front simulation experiments maintained >90% survivorship through the completion of the first cold-front event, which included a 24- or 48-h exposure to 3°C. Higher survivorship occurred despite exposure to simulated cold-front events that were characterized by 1°C temperature decreases every 9 h compared with more gradual (1°C d^{-1}) reductions in water temperature during thermal-tolerance experiments. Despite the more rapid rate of temperature decline, the brevity of the exposure yielded a survival advantage for fish during the cold-front simulations. Similar to our findings during the thermal-tolerance experiments, Ma *et al.* (2007) observed that the mortality of juvenile red drum had reached 50% within 24 h of exposure to 3°C. The temperatures in their study had been decreased gradually from 12 to 3°C over 18 d (1°C 2 d^{-1}), resulting in prolonged exposure to cold temperatures before reaching 3°C. These findings support the notion that cumulative exposure to stressful water temperatures is the primary driver of increased mortality. The importance of cumulative exposure to temperatures near the lower lethal limit has also been suspected to be a major factor determining mortality rates for other temperate fish (Hurst and Conover, 1998; McCollum *et al.*, 2003; Fetzer *et al.*, 2011). For red drum, perhaps minimizing exposure to any temperatures <5°C may be more beneficial to survival than sufficient acclimation to cold conditions.

Another potentially important aspect of winter severity that may impact survivorship is the temporal spacing of cold-front events. During our thermal-tolerance experiments, all fish expired within 6 d of reaching 3°C. Fish exposed to a high frequency of long-duration, cold-front events experienced thermal minima for 48 h during each of three events, resulting in six cumulative days held at 3°C. Despite equivalent durations held at 3°C, fish in the simulated cold-front experiment realized a survival rate of 17% compared with 0% in the thermal-tolerance experiment. The amount of time between each cold-front event, when fish were exposed to rising and falling temperatures, though brief, appeared to provide fish with some relief from the effects of cold stress. It is unclear whether this represented a recovery period or if experiencing rapidly changing temperatures each day acclimatized fish to the cold-front events. Perez-Dominguez *et al.* (2006) exposed recently settled red drum to either diel fluctuations or constant temperatures, followed by a simulated cold-front event (10°C decrease in 24 h). Fish that had experienced daily thermal rhythms maintained higher survivorship during the subsequent rapid-cooling event. Thus, exposure to low and fluctuating temperatures during the diel cycle may provide thermal acclimation, meaning that previous exposure to mild cold-front events could enhance survivorship during more extreme events. Alternatively, repeated exposure to extreme temperatures with only relatively short refuge periods may still result in high rates of mortality. Juvenile red drum exposed to a high frequency of simulated cold-front events in this study experienced an increased risk of mortality with each successive event (Figure 5). This may mean that time spent at temperatures above lower lethal limits needs to be of sufficient duration to enable the recovery of physiological function and promote survival. When comparing our cold-front-event treatment levels, those that included a longer period between successive cold-front events generated the higher survivorship of juvenile red drum, suggesting that fish are able to survive multiple cold-front events, provided that they are short in duration and with ample recovery time between them.

Size-dependent response to acute cold stress

When subjected to prolonged exposure to extreme cold temperatures or severe winter conditions, red drum showed no size-dependence in survivorship. However, when exposed to moderate or mild winter conditions, larger red drum juveniles experienced higher survivorship. Size-dependent patterns of overwinter mortality have been detected for a large number of freshwater and estuarine fish, with the vast majority of studies documenting higher survivorship for larger individuals (e.g. Post and Evans, 1989; Pangle *et al.*, 2004; Michaletz, 2010). Most evidence points to starvation as the primary mechanism of size-dependent overwinter mortality, due to the combination of higher weight-specific metabolic rates and lower lipid reserves in smaller individuals (Hurst, 2007). In cases where acute cold stress is the suspected cause of death, the evidence for size-dependence is equivocal. Hurst and Conover (2002) detected no effects of body size on juvenile striped bass survivorship when exposed to ambient winter conditions as well as simulated cold-front events. Similarly, McCollum *et al.* (2003) found no difference in survival between large and small age 0 white crappies (*Pomoxis annularis*) that were suspected to have died as a result of osmoregulatory failure during winter. In contrast, and similar to our findings, both Fetzer *et al.* (2011) and Johnson and Evans (1996) observed greater susceptibility to acute cold stress for smaller individuals. Some evidence also exists for larger individuals suffering higher rates of mortality when faced with acute cold stress (Lankford and Targett, 2001).

Whether the suspected cause of death is starvation (Michaletz, 2010) or acute cold stress (McCollum *et al.*, 2003), the size-dependence of overwinter mortality is more pronounced during milder winters. Our findings for juvenile red drum support this idea. When fish were subjected to prolonged exposure to extreme cold temperatures, both large and small individuals

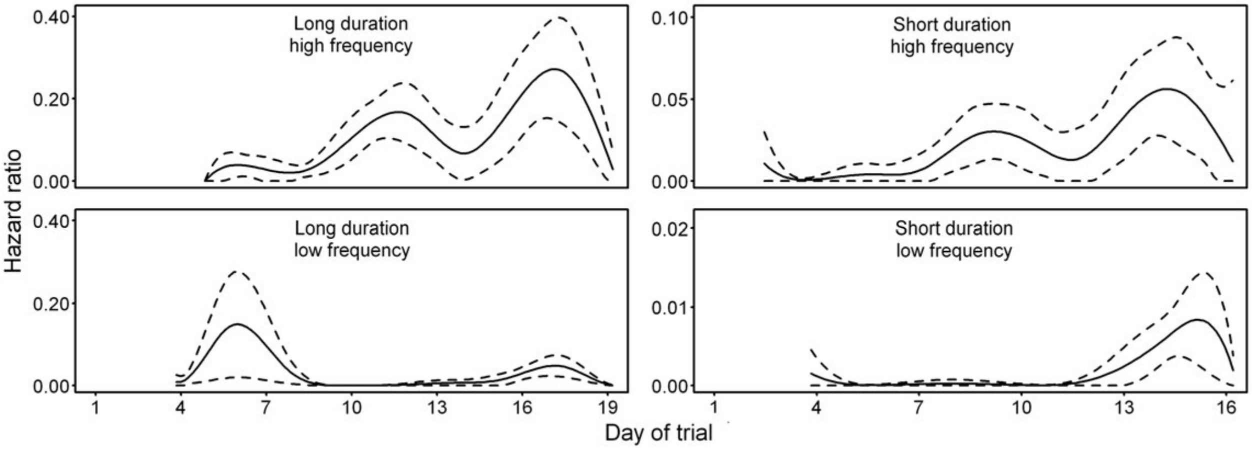

Figure 5. Cox proportional hazard ratios relative to time of trial for each cold-front-event simulation. Note the differences in the scale of the *y*-axes which reflects differences in the overall magnitude of the hazard ratios among winter severity simulations.

experienced low survivorship. Similarly, during exposure to the most severe winter conditions based on the frequency and the duration of cold-front events, mortality of juvenile red drum was not dependent on body size. Only during exposure to moderate and mild winter conditions did we see evidence of size-dependent mortality, with larger fish realizing higher survivorship. When conditions are most extreme, the combined effects of minimum water temperature and exposure time can exceed survival thresholds of all individuals, regardless of body size, resulting in size-independent overwinter mortality (Fetzer *et al.*, 2011). Hurst and Conover (1998) observed clear size-dependence in overwinter mortality of juvenile striped bass only during the mildest winter that they analysed and suggested that the strength of size-selective mortality should be expected to vary with winter severity for most temperate fish. We suspect that the importance of body size in shaping overwinter mortality patterns of juvenile red drum is likely to vary considerably from year to year based on climatic fluctuations.

For first-year fish, cohort demographic traits such as age and growth rate can also often contribute to variation in overwinter mortality because of their role in determining body size distributions at the onset of winter. In the US Mid-Atlantic, red drum spawning may begin as early as mid-July and extend until late October (Ross *et al.*, 1995; Stewart and Scharf, 2008). Later hatching times coupled with reduced growth potential at colder autumn water temperatures (Lanier and Scharf, 2007) can lead to small body sizes for some individuals before winter. When combined with variable autumn growth among individuals, the moderately protracted spawning season of red drum can typically generate prewinter size distributions with up to threefold variation (Martin, 2009). While hatch timing may primarily be driven by abiotic processes, individual growth rates are often also influenced by multiple biotic processes. Dense cohorts can compete for limited food and experience reduced growth during the first year of life, providing a template for size-selective overwinter mortality (e.g. Martino and Houde, 2012). Early hatch timing increases the length of the growing season before the first winter and usually provides access to optimal growth conditions for the longest duration, which has been found to produce higher overwinter survival for several fish species (Henderson *et al.*, 1988; Ludsin and DeVries, 1997; Post *et al.*, 1998). For species like red drum that spawn during late summer and early autumn, hatch timing and autumn growth conditions may be especially critical for determining not only the strength of size-dependence, but also the overall magnitude of overwinter mortality in a given year.

Recruitment implications

The influence of environmental variability on the population dynamics of marine fish is often strongest near the edges of a species' distribution. In a review, Myers (1998) found that environment–recruitment correlations were most robust near the limits of a species' geographical range. Fish living near their range limits are expected to respond more directly to abiotic processes and thus display greater variability in recruitment and population density. Although the range of red drum has extended up to Massachusetts in waters along the US Atlantic coast (Hildebrand and Schroeder, 1927), currently they are only rarely encountered north of Virginia. Moreover, the consistent presence of first-year juveniles has only been documented as far north as North Carolina. Therefore, winter conditions typical of the North Carolina coast are likely the most severe experienced by prerecruit red drum throughout their range, with the potential for greater environmental forcing on red drum population dynamics relative to fish overwintering farther south along the Atlantic coast or in the Gulf of Mexico. Several recent examples highlight the impact of winter conditions during juvenile life stages in shaping year-class success of marine fish (Hare and Able, 2007; Ojaveer *et al.*, 2011; Martino and Houde, 2012). Each of these cases involved either strong environmental forcing during cold winters or prewinter compensatory processes that facilitated the function of winter as a recruitment bottleneck. We conclude that the greatest likelihood for significant modification of red drum year classes caused by environmental variability exists at the northernmost edge of their distribution along the US Atlantic coast.

The use of fishery-independent sampling of age 0 fish to develop an index of recruitment is widely practiced within fishery resource management. However, for many marine fish species, the abundance of early larval stages can often be poorly correlated with eventual fishery recruitment; rather, late larval and early juvenile stages may provide a more reliable index of year-class success (Bradford, 1992). Because of its longer duration, processes occurring during the juvenile stage have been implicated to dampen and, in some cases, regulate the recruitment of marine fish (van der Veer *et al.*, 2000; Houde, 2008). Therefore, many recruitment indices are based on juvenile abundance surveys; however, only rarely has the performance of these indices been validated (e.g. Wilhite *et al.*, 2003). The North Carolina Division of Marine Fisheries has estimated relative abundance for juvenile red drum during autumn of each year since 1991. Bacheler *et al.* (2008) recently evaluated the performance of the index and concluded that temporal and spatial coverage was sufficient to quantify relative year-class size and that the calculation of the index was computationally sound. A positive association was noted between autumn juvenile abundance and fishery landings 2 years later, but the relationship left a considerable amount of variation unexplained. Winter mortality after the estimation of the index could contribute substantially to this variation and modify the red drum year-class size. Our experimental results indicate that juvenile red drum are most vulnerable to mortality when water temperatures remain $<5^\circ$C for extended periods or when exposed to frequent cold-front events. Size-selective mortality, and resulting restructuring of cohort demographics, is not likely to occur during the most severe winters. However, mild and moderate winter conditions may remove a greater fraction of small fish, meaning that delayed spawning or poor autumn growing conditions could exacerbate any effects of winter. Therefore, the accurate assessment of the effects of overwinter mortality on red drum year-class success will likely require both an understanding of the factors that determine prewinter size distribution and the size-dependent response to winter severity.

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