Evaluating juvenile thermal tolerance as a constraint on adult range of gray snapper (Lutjanus griseus): A combined laboratory, field and modeling approach

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ABSTRACT

Climate change is expected to cause a poleward shift of many temperate species, however, a mechanistic understanding of how temperature and species' life histories interact to produce observed adult range is often lacking. We evaluated the hypothesis that juvenile thermal tolerance determines northern range in gray snapper (*Lutjanus griseus*), a species commonly caught as juveniles along the US Atlantic coast well north of their adult distribution, using a combined laboratory, field and modeling approach. The cumulative degree days below 17 °C ($CDD{<}17$) survived by individuals maintained in the laboratory under ambient seasonal cooling conditions were used to quantify the chronic effects of prolonged but non-lethal low temperatures. Under ambient conditions, juveniles stopped feeding below 11.3 °C, and the mean temperature at death was 10.2 °C ($+/-0.74$ S.D.). The $CDD{<}17$ endured by individuals ranged from 61.9 to 138.8 ($83.54+/-22.44$ S.D.), and was positively related to fish size. The relation between $CDD{<}17$ and fish size was extrapolated to the maximum juvenile size in fall to provide an upper limit for survival in the wild ($CDD{<}17=210$ days). Acute low temperature tolerance was evaluated in a second experiment that exposed juveniles to a constant rate of temperature decline (3 °C d^{-1}), where feeding ceased at 10.3 °C and death occurred at 7.0 °C ($+/-0.45$ S.D.). These thermal thresholds were combined with winter estuarine temperature data at 12 sites to evaluate potential overwinter survival along the US Atlantic coast. Of a total of 134 site-year combinations categorized based on the acute and chronic thresholds, the $CDD{<}17$ threshold (>210 days) was more limiting than the acute threshold (minimum daily temperature${<}7.0$ °C) to survival of juveniles for a given site-year. To evaluate the relationship between juvenile thermal tolerance criteria and adult distributions, we quantified adult distribution using field observations in the western Atlantic Ocean compiled from a database of recreational divers. There was a strong correspondence between observations of adult gray snapper from the database of recreational divers vs. latitude with that of the predicted survival of juveniles vs. latitude from our analysis. The agreement between the laboratory-derived thermal tolerance metrics, the spatial distribution of winter temperature, and the distribution of adult gray snapper support the hypothesis that the adult range of gray snapper is largely limited by the overwinter survival of juveniles. Understanding the interaction between physiology and range is important for forecasting the impacts of climate change on other species of fish where juvenile tolerances are critical in determining range, particularly in seasonal systems.

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1. Introduction

Marine organisms can expand their range through several dispersal mechanisms. Early life stages (eggs, larvae, and juveniles) can be transported beyond the adult range and subsequently survive and reproduce (Pineda et al., 2007). Movement during one or more later life stages (juvenile and adult) with subsequent survival and reproduction also can result in range expansion. These juvenile and adult movements can take many forms including ontogenetic shifts in habitat and seasonal migrations (Rountree and Able, 2007), each of which presents opportunities for range expansion depending on the scale of the movement. Species-specific life histories dictate which life stages have the greatest dispersal potential thereby affecting range expansion of the population as a whole. At one end of the life history spectrum, many marine invertebrates (e.g., surf clam, scallop, etc.) disperse widely as eggs and larvae, but once they settle as juveniles, there is little or no potential to alter their spatial distribution (Palmer et al., 1996; Weinberg, 2005). For

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such species, range expansion of adults is limited by early life stage dispersal. In contrast, at the other end of the spectrum, highly migratory (pelagic) species of fishes (e.g., tunas) are able to seek out (and occupy) suitable adult habitats regardless of the distribution of early life stages (Brill et al., 1999; Fromentin and Powers, 2005). For species with highly mobile adult stages, the adult range may be largely determined by the distribution of suitable habitat and the specific migration ability of adults.

Many subtropical and tropical fishes are delivered, as larvae, to seasonally tolerable temperate systems around the world (James et al., 2008) including the western North Atlantic where planktonic transport pathways are influenced by the Florida Current–Gulf Stream (Hare and Cowen, 1991, 1996; Hare and Walsh, 2007; Hare et al., 2002). There are three potential outcomes of this long-distance dispersal. First, the early life stages may survive, grow to maturity, and reproduce thereby extending the adult range. This possibility is limited by the factors that first affect juvenile and subsequently affect adult mortality. Second, larvae may survive and attain the necessary size to successfully migrate back to subtropical waters and rejoin adult populations in advance of autumn cooling in temperate latitudes (e.g., crevalle jacks, McBride and McKown, 2000; bluefish and white mullet, Able et al., in press; gag grouper, Ross and Moser, 1995). In these cases, spawning, settlement or both occur early enough in the year to exploit suitable (summer) temperatures at higher latitudes and return migration occurs before waters become too cold for survival. Third, larvae and juveniles may survive into the fall, but lacking the ability to migrate southward, individuals perish as a result of thermal tolerance limitations, starvation or predation (e.g., butterflyfishes, McBride and Able, 1998). These early life stages are generally considered to be 'expatriates' (i.e., lost from the population that spawned them) and overwinter mortality of juveniles is thought to limit the successful expansion of adult range.

Climate change due to increased concentrations of greenhouse gases is expected to result in increased ocean water temperatures in many systems (Kordas et al., 2011; Philippart et al., 2011; Scavia et al., 2002). The gradual poleward expansion of tropical and sub-tropical species as temperatures increase has been documented from adult distributions for many species (Fodrie et al., 2010; Hare and Able, 2007; Mountain, 2002; Murawski, 1993; Nye et al., 2009; Parker and Dixon, 1998), however, a mechanistic understanding of how temperature and species life histories interact to produce observed adult range is often lacking. Given that larval supply already exists along the US Atlantic coast for many subtropical species, and winter severity has decreased in the region in recent decades (Able and Fahay, 2010; Hare and Able, 2007), overwinter juvenile mortality of many subtropical species in temperate systems may diminish, thereby facilitating poleward expansions of their ranges.

In this study, we focus on gray snapper (*L. griseus*) along the US Atlantic coast, where they occur as juveniles in temperate nearshore habitats at the end of summer, and evaluate whether overwinter survival of young-of-the-year limits the poleward range. The northernmost aggregations of adult gray snapper occur at reefs offshore of central Florida (Chester et al., 1984) and larvae are transported north via the Gulf Stream and associated flows (Hare and Walsh, 2007). The supply of ingressing larvae and juveniles is well documented in North Carolina (Denit and Sponaugle, 2004; Tzeng et al., 2003; Wuenschel et al., 2004, 2005) and during summer and fall juveniles are reported from Massachusetts southward (Able and Fahay, 1998, 2010; Sumner et al., 1913), where they settle into estuarine and nearshore habitats. Many tropical fishes that utilize shallow sea grass and mangrove nurseries are considered hyperthermal specialists (Eme and Bennett, 2009; Eme et al., 2011).

Limited survival of juvenile gray snapper north of Florida is suggested by the extreme rarity of adults on reefs (hard or 'live' bottom) from Georgia to North Carolina (Burton, 2001; Chester et al., 1984; Cuellar et al., 1996; Parker and Dixon, 2002; Schobernd and Sedberry, 2009). Anecdotal data on lower temperature tolerance of gray snapper is available (Starck, 1971; Tzeng, 2000), as are reports of winter kills

from the Gulf of Mexico (Holt and Holt, 1983; Tolan and Fisher, 2009; http://research.myfwc.com/fishkill/; http://myfwc.com/media/316259/Saltwater_FishKillsFAQs.pdf). Recent studies have investigated the energetics (i.e., feeding, growth and metabolism; Wuenschel et al., 2004, 2005) of juvenile gray snapper at temperatures representative of their subtropical range (18–33 °C), however, the response of juvenile gray snapper to lower temperatures, more typical of US Atlantic coast estuaries during fall is lacking. The goals of this study were to 1) experimentally determine low temperature thresholds for feeding and survival of juvenile gray snapper, 2) combine those temperature thresholds with estuarine temperature data to evaluate potential overwinter survival along the US Atlantic coast, and 3) compare predicted distribution of overwinter juvenile survival to observed adult distribution.

2. Methods

We studied two aspects of the thermal tolerance of gray snapper. First, to evaluate cumulative (chronic) effects of low (but non-lethal) temperatures, we quantified the total degree days below a physiological threshold temperature survived by individuals held in ambient cooling conditions. Second, we quantified the chronic lethal minimum temperature (Beitinger et al., 2000; Bennett et al., 1997; Kimball et al., 2004) at a constant rate of temperature decline (3 °C day^{-1}).

Juvenile gray snapper were collected in the Mullica River–Great Bay estuary with a beach seine October 2–4, 2007 (see Able and Fahay, 1998, 2010 for a detailed description of the study area). Specimens were placed in containers filled with ambient water (19.7–22.1 °C), and transported to the Rutgers University Marine Field Station (RUMFS), where experiments were carried out. At RUMFS, fish were held in two large aquaria provided with artificial structure, fed daily and allowed to acclimate to the laboratory for 5 d prior to beginning experiments.

2.1. Experiment 1 — ambient conditions of seasonal cooling

Individual fish were measured (total length; mm), weighed (g), and randomly stocked into individual 8 liter solid walled containers provided with structure (section of PVC pipe) and aeration on day 1 (10/08/2007). Photoperiod was maintained at 12L:12D; ambient photoperiod was approximately 11L:13D. Containers were placed in one of two water tables. One randomly chosen group, hereafter referred to as the ambient group ($n = 15$), were placed in a water table supplied with ambient seawater. Analysis of temperature data loggers (Tidbit Temp Logger, Onset Computer Corp., Pocasset, MA) deployed simultaneously indicated the ambient seawater in the water table averaged 0.63 °C ($+/-0.84$ S.D.) warmer than the estuarine source during the experimental period. A second randomly chosen group ($n = 10$), were placed in a heated water table (~20 °C) to serve as controls. The control tanks were maintained at a temperature above the lower limit estimated for growth (i.e., 17–18 °C; Wuenschel et al., 2004), and within the range of temperatures 18–33 °C that juveniles have been reared for prolonged periods with minimal mortality (Wuenschel et al., 2004, 2005). Temperature and salinity of each container ($n = 25$) was recorded daily with a temperature-conductivity meter (YSI model 85, Yellow Springs Instruments, Yellow Springs, OH). In addition, temperature dataloggers were placed in each water table and within one experimental container in each table to provide continuous temperature records (every 30 min) during the experiment. Fish were fed thawed brine shrimp daily and live wild zooplankton and small decapod crustaceans when available. Feeding behavior of individuals in both ambient and control groups was recorded daily. Additional observations of fish behavior were noted, and any mortalities were removed and measured. Individual containers were cleaned then followed by water changes (approximately 1/3 of container volume) three times per week. Individual container salinities averaged 33.9 ($+/-2.5$ S.D.) during the experiments. After the start of the experiment, ambient temperatures rose slightly, therefore we re-measured

individuals (length and weight) on day 14 (10/22/2007) so that we could account for growth during this unanticipated warm period.

The weight of fish each day (W_t) was estimated (between measurements made at day 1, day 14, and death) assuming exponential growth (Ricker, 1979): $W_t = W_0 e^{Gt}$, where W_0 = initial body weight, G = instantaneous daily growth coefficient [$(\ln W_t - \ln W_0)/\text{days}$]. Observations of daily feeding behavior of individuals (*Yes* or *No*) were modeled using repeated measures logistic regression (PROC GENMOD SAS) with a logit link function, which is appropriate for longitudinal binomial data. The method provides parameter estimates from generalized estimating equations fit to the clustered categorical data with standard errors, confidence intervals, *Z* scores and *P*-values based on empirical standard error estimates (SAS OnlineDoc Version 8, p1452–1455, v8doc.sas.com/). The logistic regression model analyzed repeated measures of feeding and non-feeding of individuals at the full range of daily temperature observations. Since the control group continued to feed throughout the experiment, and temperatures were relatively constant, only the ambient group was modeled. The probability of feeding was modeled using a binomial distribution and logit link function with temperature and the estimated fish weight on that day as explanatory variables.

To evaluate chronic effects of prolonged low (but non-lethal) temperatures and to incorporate both temperature and time into a single metric integrating thermal tolerance of gray snapper, we used a cumulative degree day metric (thermal integral) that has been widely applied in agricultural and entomological studies but less so in fish studies (Neuheimer and Taggart, 2007). Specifically, we calculated the cumulative degree days below a critical physiological threshold temperature. A threshold temperature of 17 °C was chosen for degree day calculations, since this is the temperature estimated by Wuenschel et al. (2004) where growth of juvenile gray snapper ceases even with unlimited food. Cumulative degree days below 17 °C survived ($CDD{<}17$) by individuals were calculated for individual fish as follows:

$$CDD < 17 = \sum_{t=1}^{t=n}(17 - Temp_t)$$

where $Temp_t$ is the daily mean water temperature on day t and n is the number of days from the start of the experiment to death.

2.2. Experiment 2 — constant rate of temperature decline

After all fishes in the ambient group of Experiment 1 died, survivors from the control group ($n = 7$) were used for the second experiment. Fishes were exposed to a constant rate of decline in water temperature (3 °C day^{-1}) following chronic lethal methodology with death as the endpoint (Beitinger et al., 2000; Bennett et al., 1997; Kimball et al., 2004). The temperature controlled water bath was manipulated to achieve a 3 °C day^{-1} decline in temperature in the individual containers. Temperatures and observations of feeding and swimming equilibrium were recorded several times daily for each fish. Fishes were considered dead when all fin, body, and opercular movements ceased and they did not respond to physical stimuli (i.e., prodding with a probe) (Kimball et al., 2004; Lankford and Targett, 2001a, b).

2.3. Thermal thresholds for gray snapper

A chronic thermal threshold was estimated using the cumulative degree days below 17 °C survived ($CDD{<}17$) by individuals under ambient cooling in Experiment 1. The juvenile gray snapper utilized in thermal tolerance experiments were smaller in size than juveniles collected in US east coast estuaries in other studies (Denit and Sponaugle, 2004). To account for an expected increase in thermal tolerance with size, we extrapolated the observed relationship between $CDD{<}17$ and fish weight (see Results section below) to the largest size collected north

of Florida by Denit and Sponaugle (2004; 4.69 g). This approach provides a conservative upper bound of chronic thermal tolerance. The mean lower lethal limit observed in Experiment 2 was assumed to represent acute thermal tolerance. Together, these chronic and acute thermal thresholds were applied to analyses of estuarine water temperatures (below).

2.4. Winter water temperature observations for US Atlantic coast estuaries

Daily water temperature records for estuarine systems along the US Atlantic coast were accumulated from several sources (see Supplementary material). Data were first visually inspected and then observations greater than 35 °C and less than 0.5 °C were discarded. Daily climatologies were calculated for each site and daily observations that differed more than $+/-5$ °C from this daily climatology were discarded. Data were interpolated with a nearest neighbor algorithm at a daily interval to fill missing values. Years that did not have near complete temperature records during the fall, winter, and spring were not used in the analysis. In all, data from 12 sites were used with an average of 13 years of useable data per site.

The cumulative degree days below 17 °C ($CDD{<}17$ as above) was calculated for each site and year combination (chronic limit). The minimum mean daily temperature also was determined for each winter at each location in the time series (acute limit). Potential overwinter survival for each site-year combination was determined based on the chronic and acute thermal tolerance thresholds determined above.

2.5. Summary of field observations of adult snapper to determine current range

To evaluate the relationship between juvenile thermal tolerance criteria and adult distributions, we quantified adult distribution using field observations of gray snapper in the tropical western Atlantic Ocean compiled from the Reef Environmental Education Foundation (REEF, http://www.reef.org). Specifically, we summarized the total number of dives and those dives observing gray snapper from 1997 to 2007 in regions extending from the Florida Keys north to Massachusetts. Year/region combinations with fewer than 10 dives were excluded from the analyses. A total of 87 year/region combinations were used in the analysis, which included information from more than 25,000 dives. There were a greater number of dives at the southern end of the study area. However, there were more than 2000 dives in northern areas ($>30°$N), so we are confident these data represent the distribution of adult gray snapper along the coast. The observation frequency of adult gray snapper vs. latitude was analyzed with a segmented binomial model to quantify the northern limit in range (Ficetola and Denoel, 2009).

We then evaluated whether the juvenile thermal tolerance metrics agreed with the northern limits of adults as a test of the hypothesis that overwinter juvenile mortality determines northern range in gray snapper. Specifically, we compared logistic regression models describing the relationship between a survivable winter and a non-survivable winter vs. latitude (from the perspective of juvenile thermal tolerance thresholds) to the northern latitude of the adult range determined from the segmented binomial model.

3. Results

3.1. Experiment 1 — ambient conditions of seasonal cooling

Gray snapper in both the ambient and control groups actively fed in captivity, and grew minimally during the first two weeks of the experiment (Table 1) when temperatures remained above 17 °C indicating these conditions were favorable for growth. Individuals in the control group continued to grow throughout the trial, however,
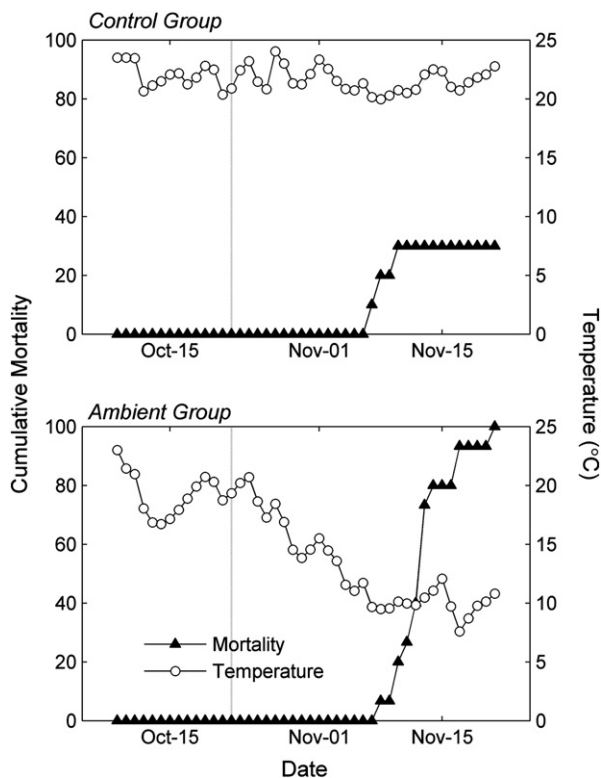
Table 1
Juvenile gray snapper characteristics for the control and ambient decline groups for Experiment 1. Size and weight are reported for the beginning of Experiment 1 (day 1) and after two weeks (day 14). Specific growth rates (SGR) are reported for two time intervals: interval #1 (10/08/2007 to 10/22/2007); interval #2 (10/20–22/2007 to death). Temperatures at feeding cessation and death and total degree days below 17 °C survived are reported for the experimental group. Where possible, values are reported as means +/− S.D. (range). *P* values are reported for *t*-tests (2-tailed) between control and ambient groups.

Variable	Control (n = 10)	Ambient (n = 15)	P
Day 1 — length (mm TL)	31.12 +/− 8.13 (25.1–52.1)	31.45 +/− 6.9 (22.3–45.7)	0.916
Day 1 — weight (g)	0.513 +/− 0.522 (0.20–1.91)	0.522 +/− 0.38 (0.17–1.51)	0.963
Day 14 — length (mm TL)	31.57 +/− 8.65 (25.1–53.7)	31.52 +/− 7.19 (22.5–46.2)	0.988
Day 14 — weight (g)	0.596 +/− 0.574 (0.25–2.16)	0.578 +/− 0.40 (0.23–1.64)	0.935
Interval #1 SGR (% weight g day^{-1})	1.36 +/− 0.77	0.97 +/− 0.74	0.219
Interval #2 SGR (% weight g day^{-1})	0.53 +/− 0.83 [0.98 +/− 0.39][a]	−0.046 +/− 0.35	0.062 [<0.001][a]
Temperature at feeding cessation (°C)	N/A	11.3 (11.1–11.5)[b]	
Temperature at death (°C)	N/A	10.167 +/− 0.743 (8.6–10.9)	
CDD<17 (cumulative degree days <17 °C until death)	N/A	83.54 +/− 22.44 (61.9–138.8)	

[a] Survivors only (excluding the 3 early mortalities).
[b] 95% C.I. interval predicted from the logistic regression model.

three individuals died of causes presumably unrelated to temperature (Fig. 1). These three individuals stopped feeding, displayed erratic swimming, and showed signs of distress (heavy ventilation) for a period of 1–2 days before dying. Also, these fish died at relatively warm temperatures (19.0–20.2 °C) and their behavior differed from those of cold-stressed fish, therefore their deaths were assumed to be unrelated to temperature. Juvenile gray snapper in the ambient group showed negative growth after day 14 and began to die when the temperatures approached 10 °C (Fig. 1). Fish showed signs of stress including darkened pigmentation and sheltering in and under the provided structure. Cold-stressed fish eventually lost equilibrium and remained motionless on their side on the bottom of the container. This motionless state persisted for hours to days in some cases, and some individuals rebounded from this moribund state if ambient temperatures increased slightly.
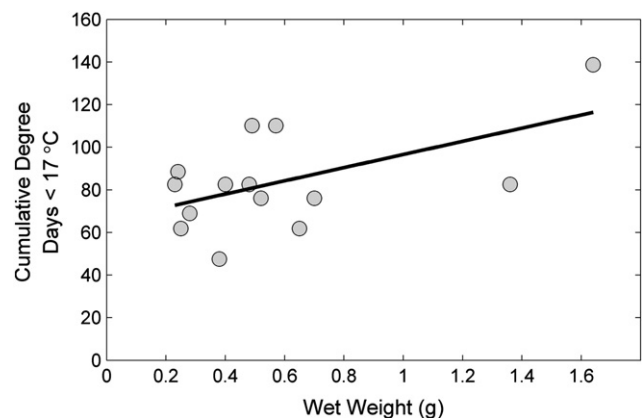
The mean temperature at death was 10.2 °C (+/− 0.75 S.D.) without a significant effect of fish size. Although larger fish did not survive colder temperatures, they did survive longer (Fig. 2), and therefore experienced greater duration of low temperatures before death. Although the r^2 for the regression of CDD<17 vs. weight was low ($r^2 = 0.31$), the model parameters were significantly different from zero (P<0.05). All of the fish in the ambient group died within a two-week period (11/8/2007–11/21/2007). The repeated measures logistic regression model (generalized estimating equations fit to 450 observations from 15 clusters [individuals]) estimated a 50% probability of individuals feeding at ~11.3 °C (Fig. 3), and the probability rapidly decreased or increased at temperatures below or above this value respectively. Temperature had a significant effect on the probability of feeding (P<0.01), but the effect of fish weight was not significant (P = 0.94).

3.2. Experiment 2 — constant rate of temperature decline

Gray snapper (n = 7, mean weight = 0.6 g +/− 0.26 S.D., range = 0.30–0.98 g) ceased feeding at ~10.3 °C (+/− 0.32 S.D., range = 9.9–10.7 °C), and died at 7.0 °C (+/− 0.45 S.D., range = 6.6–8.0 °C) when exposed to a constant rate (3 °C day^{-1}) of water temperature decline. Cold-stressed gray snapper lost equilibrium and were observed on their sides on the bottom of the container for a period of time before eventually ceasing all fin and opercular movement at death. As in Experiment 1, fish weight did not have a significant effect on the temperature at cessation of feeding (P = 0.12) or lower critical thermal minima (P = 0.17), however, larger fish did appear to achieve slightly lower critical thermal minima (Fig. 4).

3.3. Thermal thresholds for gray snapper

Extrapolating the observed relationship between CDD<17 and fish weight (Fig. 2) to the largest sizes collected north of Florida during the fall (data from Denit and Sponaugle, 2004) provided a CDD<17 estimate of ~210. The mean lower lethal limit observed in Experiment 2 was 7.0 °C. Together, these chronic (CDD<17 = 210) and acute (water

Fig. 1. Mean daily water temperature (circles) and cumulative mortality (triangles) for the control (top) and ambient (bottom) groups. Vertical gray line denotes point at which individuals were re-measured.

Fig. 2. Cumulative degree days below 17 °C (CDD<17) survived in relation to wet weight on day 14 for individual gray snapper from the ambient group in Experiment 1. Model: CDD<17 = 65.67 + 30.92 ∗ Weight, $r^2 = 0.31$, n = 15.
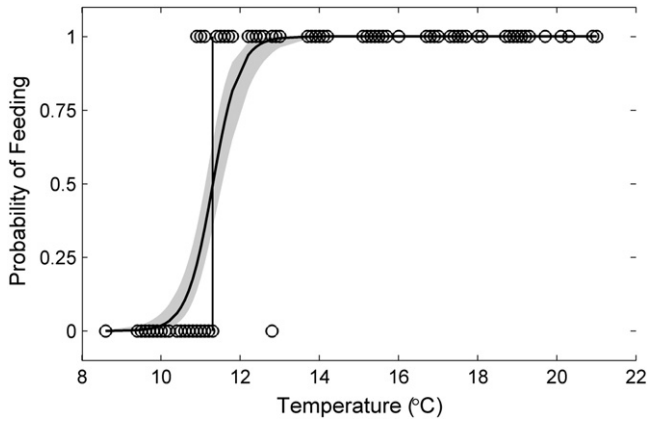
Fig. 3. Probability of feeding across temperatures determined by repeated measures logistic regression model (heavy line). Points indicate individual observations (feeding = 1 and non-feeding = 0) for the ambient group over the course of Experiment 1 (15 individuals, 450 observations). Shaded area represents 95% confidence interval for the regression.

temperature = 7.0 °C) thermal thresholds were used to determine overwinter survival of juvenile gray snapper at estuarine sites (below).

3.4. Winter water temperature observations for US Atlantic coast estuaries

The cumulative degree days below 17 °C (CDD<17) for coastal waters on the US east coast was related to the minimum daily winter water temperatures for each site-year (Fig. 5[A,B], Spearman's rank correlation = −0.92, P<0.001). A strong latitudinal pattern in CDD<17 was evident, ranging from 0 at southern sites to over 2000 at the northern sites. Within the larger-scale latitudinal pattern, year to year variability was evident and synchronized across sites (Fig. 5[C,D]). The time series of CDD<17 were correlated among sites, even those separated by >500 km indicating large-scale coherence (Fig. 6). The time series of minimum daily winter temperature exhibited coherence at shorter spatial scales, and at distances >300 km correlations between sites were low.

Winter temperature data for the 134 site-year combinations were categorized using the following criteria; winter minimum temperature above or below 7.0 °C (the acute low temperature tolerance estimated above), and CDD<17 above or below 210 days (the chronic thermal tolerance limit estimated above) (Table 2). For site-years without chronic thermal limitation (CDD<17 below 210 days), minimum winter temperatures were always above the acute threshold (7.0 °C). However, for site-years with chronic thermal effects (CDD<17 below 210 days), the
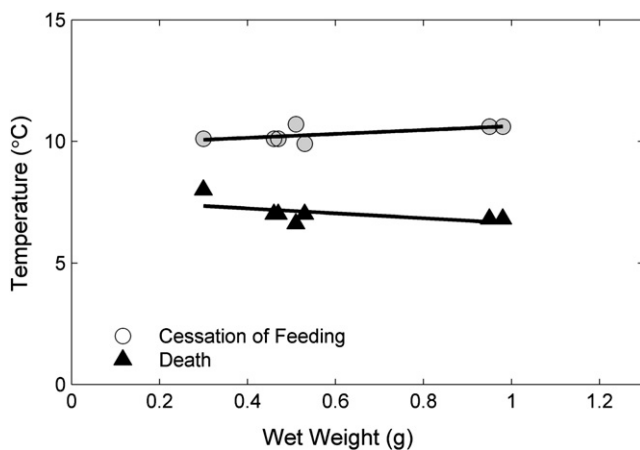
Fig. 4. Cessation of feeding (circles, $n = 7$, $r^2 = 0.41$) and critical lethal minimum (triangles, $n = 7$, $r^2 = 0.51$) temperatures (°C) for gray snapper from Experiment 2.

winter minimum temperature was below the acute thermal limit in most but not all years (Table 2). Thus, the CDD<17 threshold is a more restrictive (conservative) approach for estimating the survival probability of juvenile gray snapper for a given site-year.

### 3.5. Summary of field observations of adult snapper to determine current range

The poleward limit of adult distribution corresponds with the latitude where the combined thermal criteria are exceeded (Fig. 7). Observation frequencies of gray snapper were high to approximately 30°N and then dropped off further poleward. The segmented binomial model predicts that the break in gray snapper distribution occurs at 29.5°N (+/− 0.83 S.E.). The logistic models for the thermal tolerance criteria indicated a 0.5 frequency of survivable winters at 30.4, 32.6, and 30.1°N for the cumulative degree day, minimum daily temperature, and the combined thresholds, respectively. The shape of the combined threshold suggests a steep break in the location of survivable winters (30.1°N) and this break corresponds closely to the estimate poleward limit of adults (29.5°N).

4. Discussion

Along the east coast of the United States, larvae of gray snapper, and many other species, are transported well poleward of their adult range (e.g., Able and Fahay, 2010; Hare and Cowen, 1991). Juvenile gray snapper, and other species, settle into coastal habitats, grow and survive through the summer and early fall (e.g., Able and Fahay, 2010; Denit and Sponaugle, 2004; McBride and Able, 1998; Wood et al., 2009). Here we evaluated the hypothesis that juvenile thermal tolerance determines northern range in gray snapper. As temperatures drop below the cold water thermal tolerance in fall, juveniles die and the winter distribution of coastal temperatures determines the northern limit of juveniles surviving in the spring. Since gray snapper do not make substantial along-shelf migrations (Jones et al., 2010; Luo et al., 2009), the juvenile distribution establishes the adult distribution. We documented coldwater tolerance, and then evaluated the latitudinal distribution of temperature patterns relative to the gray snapper thermal limits. We found that the distribution of temperatures was closely linked to the distribution of adults, thereby supporting the hypothesis that juvenile thermal tolerance determines northern range in gray snapper. The broader applicability of this hypothesis has yet to be evaluated, but juvenile thermal tolerance as a controlling factor could be critical for the many marine species with planktonic larvae and relatively sedentary juvenile and adult stages.

An important aspect of thermal tolerance is the difference between acute and chronic limits. For juvenile gray snapper, we found the acute limit to be ~7.0 °C whereas we estimated a chronic limit of ~210 cumulative degree days below 17 °C. Comparing these limits to observed temperatures from juvenile nursery habitats, we found that the chronic limit is more ecologically relevant than the acute limit; this finding is consistent with other studies. In the absence of predators, juvenile gray snapper were shown to survive temperatures as low as 5.7 °C for brief periods (<1 day; Tzeng, 2000) implying that if the chronic limit is not exceeded, brief exposures below the acute limit can be tolerated. Starck (1971) observed gray snapper alive at temperatures of 11.7 °C during a cold spell in the Florida Keys. In Texas bays, recent increases in the abundance of gray snapper have been attributed to warmer winter water temperatures providing more favorable over-wintering conditions (Tolan and Fisher, 2009). Finally, in northern Gulf of Mexico seagrass beds, the increase in abundance of gray snapper (by ~100 fold) has been linked to warmer temperatures (Fodrie et al., 2010).

In this study, the temperature at which feeding ceased for juvenile gray snapper was 11.3 °C. The mean temperature for cessation of feeding in the constant rate of decline experiment was ~1 °C lower (10.3 °C) than the 50% probability from the logistic model (11.3 °C). The logistic
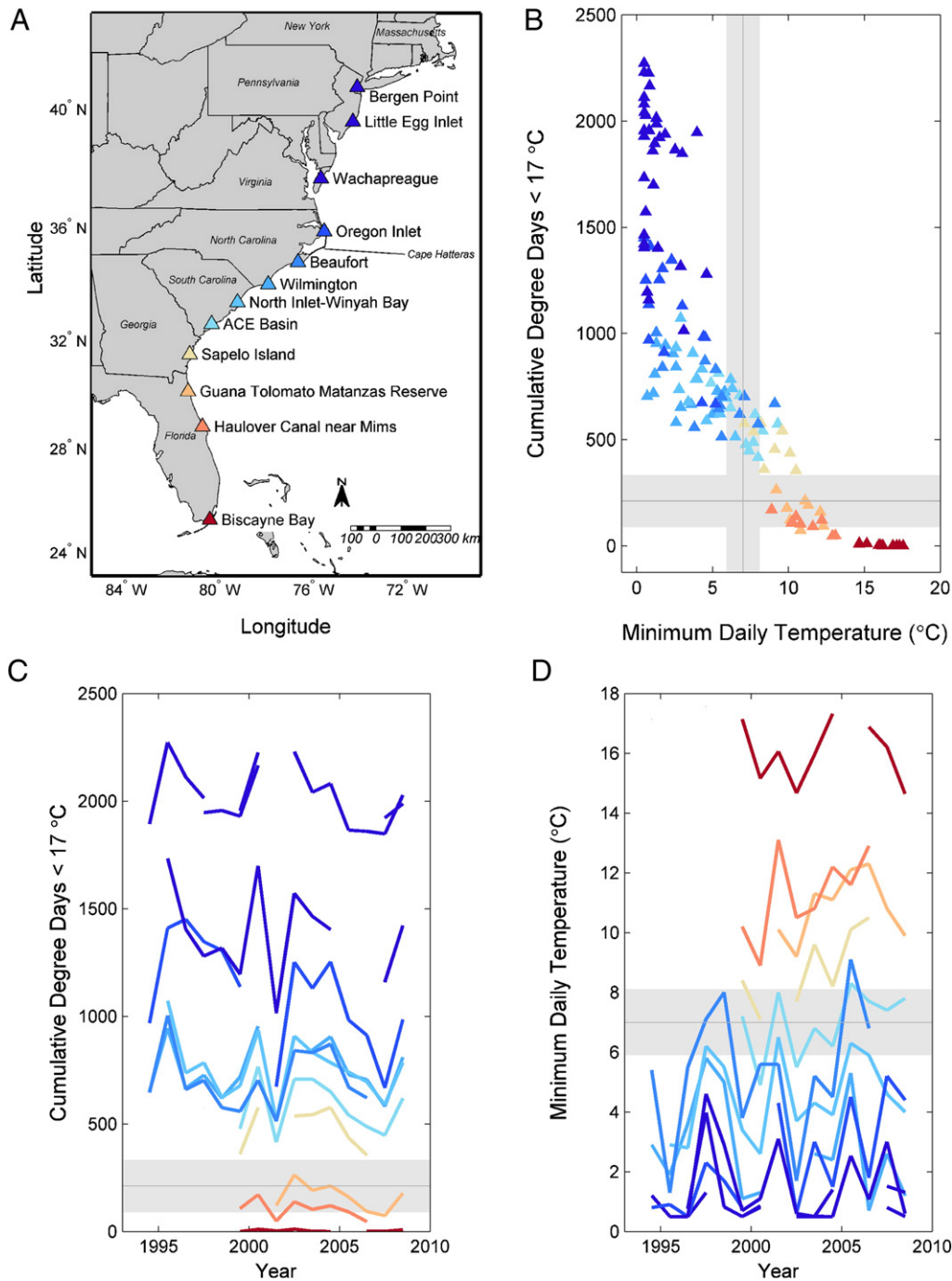
Fig. 5. Estuarine locations where coastal winter water temperatures were recorded and analyzed on the US east coast (A); relation between cumulative degree days below 17 °C (CDD<17) and minimum daily winter temperatures observed for each site-year combination (B, $n = 134$); time series of cumulative degree days below 17 °C (CDD<17) (C) and minimum daily winter water temperature (D) for 12 sites on the US Atlantic coast. Color-coding for sites is based on latitude (red more southern, blue more northern). Vertical and horizontal lines indicate chronic (CDD<17 = 210 days) and acute (minimum daily temperature = 7.0 °C) thermal thresholds, respectively. Shading represents 95% confidence intervals on estimates.

model predicted about a 5% probability of feeding at 10.3 °C. The two approaches produced slightly different, but comparable results. The logistic model is based on many observations of individuals under variable conditions of cooling, stable, and warming temperatures around the threshold value, in contrast to the rapid (3 °C day^{-1}) decline rate which was based on few observations of fishes only in a rapid cooling condition. Given the coarse and limited nature of feeding observations in the second experiment, we believe that the logistic model provides a more realistic estimate of the lower temperature for feeding of juvenile gray snapper in the wild.

With these results, we can now map the general response of juvenile gray snapper to a range of temperatures. With unlimited ration, juvenile growth is greatest at higher temperatures (~33 °C; Wuenschel et al., 2004). Temperature limitations start as temperature decreases below 23 °C where the conversion efficiency of ingested food to body growth is low (Wuenschel et al., 2004). Growth ceases below 17 °C (Wuenschel et al., 2004), and continued feeding offsets the costs of routine maintenance (Wuenschel et al. 2005). As temperature decreases further, feeding stops at approximately 11 °C and acute thermal death occurs at 7 °C (this study). Chronic thermal tolerance, however, occurs
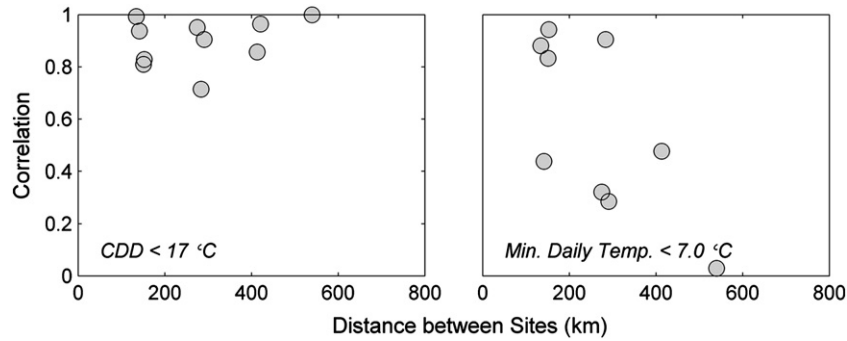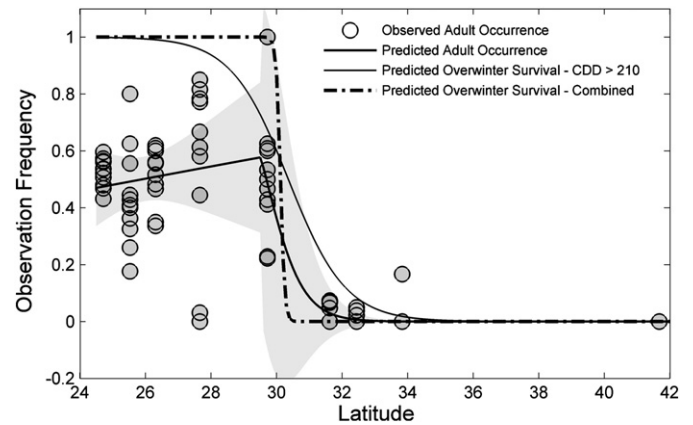
Fig. 6. Correlation coefficients (Spearman's rank correlation) between estuarine temperature time series for chronic (left) and acute (right) thermal thresholds plotted as a function of distance between daily temperature sites (see Fig. 5). Plots show the spatial correlation in thermal tolerance metrics.

when the cumulative degree days below 17 °C exceeds 210 days, and in nature this measure of thermal tolerance is more relevant; the chronic limit is exceeded before the acute limit (Table 2). Such a detailed understanding of the relationship between temperature, growth, and metabolism is not available for many species along the east coast of the United States (but see Hales and Able, 2001). Similarly, juvenile butterfly fish stop feeding when temperatures drop to 12 °C and acute death occurs at ~10 °C (McBride and Able, 1998) and lionfish stop feeding at ~16 °C and die at ~10 °C (Kimball et al., 2004). Most studies, however, have focused on acute limits and our work demonstrates that chronic limits also need to be enumerated.

There was considerable individual variability in the lethal limit of cumulative degree days below 17 °C (Table 1, Fig. 2). Some of this variability in the cumulative effects of cold temperatures is probably due to the variable (natural) temperature pattern, with brief intervals of warming and cooling within the general downward trend in temperature. Although the time until death at a constant temperature below 17 °C may have provided a less variable relationship, it would be difficult to relate this to typical seasonal patterns in fall cooling. The pattern of short periods (<one week) of warming and cooling within the longer term decline in temperature in fall is typical for many estuarine systems in the region and the CDD<17 calculation provides a common metric to evaluate survival potential under different thermal histories. Some of the variability in chronic thermal tolerance was related to weight (Fig. 2), therefore weight can and should be included as a factor in models to predict ontogenetic changes in thermal tolerance. Additional condition measures such as energy content or liver index (not measured in this study) could be easily incorporated into the modeling approach presented here. This implies that thermal tolerance is in part dependent on the ability of juveniles to grow. Denit and Sponaugle (2004) showed that juvenile growth in the field was related to temperature. The size of the gray snapper collected and used in this study were smaller than those collected by Denit and Sponaugle (2004) at a similar time of year in estuaries farther south (North Carolina to Florida), further supporting the idea of a latitudinal gradient in juvenile growth related to temperature (Denit and Sponaugle, 2004). Such a gradient will reinforce the latitudinal pattern in thermal tolerance; juveniles in northern estuaries grow slower and thus have a lower chronic thermal tolerance compared to faster growing larger juveniles farther south. Settlement time will also be important, with later settling, smaller juveniles having a lower chronic thermal tolerance (<210 days) than earlier settling, larger juveniles that have more time to grow before temperatures decline. Another factor, typically unaccounted for, is the stress associated with parasitism. Juvenile summer flounder are more susceptible to low temperature if infected by a leech (Burreson and Zwerner, 1984).

The limits for ecological death may be different than the limits for acute and chronic thermal deaths. At low temperatures (<~11 °C) juvenile gray snapper in both experiments developed darker pigmentation, eventually lost equilibrium, and finally laid motionless on the bottom. This motionless state persisted for hours to days in some cases before actual death occurred, but some individuals in the ambient group (Experiment 1) rebounded if temperatures increased slightly. Individuals in this moribund state would be easy prey for fishes and invertebrates that are more capable of operating at lower temperatures such as locally resident species. Ecological death would therefore be likely at temperatures above that determined for physiological death. These trophic considerations add further complexity to quantifying thermal tolerance, and understanding the relative importance of physiology, settlement timing, and trophic interactions may improve the estimates of the relationship between juvenile survival and temperature (see Donaldson et al., 2008; Hurst, 2007; Kordas et al., 2011). Here, we do not disentangle

Table 2
Contingency table summarizing winter temperatures for each site-year combination ($n=134$) based on the occurrence of acute (winter minimum temperatures below 7.0 °C) and chronic thermal tolerance (CDD<17 above 210 days) thresholds. The mode of thermal limitation is indicated.

Winter minimum temperature	CDD<17 below 210 days	CDD<17 above 210 days
>7.0 °C	26 Survival	20 Chronic mortality
<7.0 °C	0 Acute mortality	88 Acute and chronic mortality

Fig. 7. Observation frequency of gray snapper adults on dives along the east coast of the United States (observed adult occurrence). Data are from the Reef Environmental Education Foundation database. Also shown is the predicted observation frequency from a segmented logistic model (predicted adult occurrence) with the standard errors around this prediction shown as the shaded area. Also shown is the predicted overwinter survival of juveniles based on observed estuarine water temperatures along the coast (see Supplementary material and Fig. 5). Two thermal tolerance criteria were applied: >210 cumulative degrees days below 17 °C (CDD<17) and the combination of >210 cumulative degree days below 17 °C and minimum daily winter temperature <7 °C (combined). The close association between probability of adult occurrence and the latitudinal distribution of survivable winters supports the hypothesis that overwinter survival of juveniles controls the poleward distribution of gray snapper along the east coast.

these complex interactions, rather we estimate the acute and chronic thermal tolerances of a generic juvenile gray snapper and demonstrate that this first order estimate of thermal tolerance agrees with the northern limit of adult gray snapper, thereby supporting the hypothesis that juvenile thermal tolerance determines northern range in gray snapper.

Temperature is a major determinant of fish distributions along the southeast US Atlantic coast (Chester et al., 1984; Huntsman and Manooch, 1978; Kimball et al., 2004). Thermal gradients occur both inshore–offshore and north–south. Both gradients vary seasonally, with greater differences in winter than in summer (Chester et al., 1984). At present, it appears that these two thermal gradients (inshore–offshore, north–south) are too much for juvenile gray snapper to overcome after a brief inshore or estuarine residency during the late summer to fall nursery period. Thus, they are presumably lost from the parent population. A longitudinal study in south Florida indicated that adult gray snapper abundances on nearshore reefs were correlated to juvenile abundances in nearby mangrove habitats 1–2 years prior (Jones et al., 2010). Despite long dispersal distances during the egg and larval stages (D'Alessandro et al., 2010; Denit and Sponaugle, 2004), movements and recruitment processes during post-settlement life stages appear to occur over relatively small distances (Luo et al., 2009).

On a broader scale, there are consistent patterns in temperature variability along the US Atlantic coast. A strong relationship between minimum daily winter water temperature and cumulative degree days below 17 °C ($CDD<17$) was evident for estuaries on the east coast of the US (Fig. 5[A,B]) with tight coupling between the short (minimum daily winter temperature) and long-term ($CDD<17$) thermal measures. These two thermal measures also co-varied with both latitude and year (Fig. 5[C,D]); however, the latitudinal differences were much greater than year-to-year differences. The variation in both $CDD<17$ and minimum winter temperature was highly synchronized across sites, indicating large-scale coherence of temperatures in the region. The integrated thermal measure ($CDD<17$) was highly correlated across larger spatial scales than were single point values of minimum winter temperatures (Fig. 6). Thus, the integrated thermal measure ($CDD<17$) dampens out some of the short-term temperature heterogeneity (including lower winter temperature) that occurs at smaller spatial scales. The broad-scale coherence in temperature has also been documented for coastal temperatures along the east coast of the US (Shearman and Lentz, 2010) and for winter air temperatures over the eastern half of the US (Joyce, 2002).

For the estuary site-years analyzed, chronic (but non-lethal) temperatures appear to be more limiting for overwinter survival of juvenile gray snapper than acute lethal temperatures (Table 2). The minimum winter temperatures for some site-years were not limiting ($n=20$), but $CDD<17$ were still prohibitive for survival, as compared to only one instance where the acute limit occurred without reaching the chronic limit ($CDD<17$). The integrated thermal measure ($CDD<17$) therefore provides a more realistic (and more conservative) estimate of whether juvenile gray snapper can survive the prolonged winter period at a given site. Considering only acute lethal temperatures would overestimate the number of site-years predicted to allow overwinter survival, it is important to note, however, that the significance of behavioral and predator–prey interactions is not accounted for in this analysis. In the wild, cold-stressed fishes may have difficulty capturing prey and they are also more likely to succumb to predation by resident fishes and invertebrates more suited to winter temperatures. Nonetheless, we believe that the integrated thermal measure ($CDD<17$) provides a useful bridge from simple thermal thresholds (single lower thermal limit) to more detailed studies of feeding, behavior, and survival in the wild at low temperatures. As shown here, cumulative degree day measures can be calculated from available temperature records, and can therefore be readily applied to improve estimates of thermal effects and limitation of range for species facing changing environmental conditions (e.g., climate change) as well as examining the potential spread of introduced species (Benjamin et al., 2007). The estimates of overwinter survival in the present study

should be considered conservative since the fish utilized in thermal tolerance experiments were slightly smaller than those known to occur in many southeast US Atlantic coast estuaries during fall (Denit and Sponaugle, 2004). In addition, natural or artificial (e.g., heated effluent) thermal refuges exist within estuarine landscapes (Marcy, 2004) that may permit overwintering (albeit at a small scale), but were not considered in the present study.

Temperature is an important determinant of the occupied range of fishes, in response to either introductions (Eme and Bennett, 2008; Kimball et al., 2004) or changing environmental conditions (Fodrie et al., 2010). The realized range of fishes, however, results from the interplay of thermal effects with ontogeny (one or more life stages) and life history (dispersal). Increased ocean temperatures have permitted the range expansion of some tropical fishes in Australia (Figueira and Booth, 2009), with overwinter survival identified as a limiting factor (Figueira et al., 2009). The strong correspondence between observations of adult gray snapper from the database of recreational divers vs. latitude with that of the predicted survival of juveniles vs. latitude from our analysis (Fig. 7) provides strong support for the hypothesis that the adult range of gray snapper is largely limited by the overwinter survival of juveniles. Since gray snapper are broadly dispersed as larvae and do not undergo large-scale migrations as adults (Jones et al., 2010), we hypothesized that poleward range was limited by thermal tolerance during the juvenile stage. The agreement between the laboratory derived thermal tolerance metrics, the spatial distribution of winter temperature, and the distribution of adult gray snapper support this hypothesis. There are potentially many other species of fish where juvenile tolerances are critical in determining range, particularly in seasonal systems. Thus, understanding the interaction between physiology and range will be important for forecasting the impacts of climate change on marine fishes (see Helmuth, 2009; Portner and Knust, 2007).

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