Journal of Experimental Marine Biology and Ecology 490 (2017) 42–51

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Relating cold tolerance to winterkill for spotted seatrout at its northern latitudinal limits

Timothy A. Ellis [a,*], Jeffrey A. Buckel [a], Joseph E. Hightower [b], Stephen J. Poland [a,1]

[a] Department of Applied Ecology, Center for Marine Sciences and Technology, North Carolina State University, 303 College Circle, Morehead City, NC 28557, USA
[b] Department of Applied Ecology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695, USA

ARTICLE INFO

Article history:
Received 8 August 2016
Received in revised form 23 January 2017
Accepted 24 January 2017
Available online 16 February 2017

Keywords:
Spotted seatrout
Thermal tolerance
Natural mortality rate
Overwinter mortality
Acute cold stress

ABSTRACT

In the absence of winter thermal refugia, acute cold stress can lead to episodic mass mortality (winterkill) in fishes. Populations existing near the northern extent of a species' latitudinal range, such as spotted seatrout, *Cynoscion nebulosus* (Cuvier, 1830), in North Carolina, USA, are particularly vulnerable to winterkill. Information on cold tolerance for spotted seatrout is incomplete, which limits understanding of a likely important source of natural mortality for this species. In this study, two laboratory experiments for controlled exposure of spotted seatrout to dynamic decreases in water temperature were conducted in order to determine cold tolerance as affected by either rapid or prolonged exposure to low-temperature extremes across upper- (10) and lower-estuarine (30) salinities. Under rapid exposure, spotted seatrout were unable to maintain equilibrium at temperatures ≤ 4°C, with a small but measured mitigating effect of high salinity on the onset of observed physiological stress. No fish survived prolonged exposure (2 d) to 3 °C but spotted seatrout were tolerant of exposures to 5 °C for approximately 5 d, after which survival precipitously declined. Survival after 10-d exposure to 7 °C was high but not absolute. Salinity had no measured effect on mortality rates in the prolonged exposure trials. These empirical estimates of low-temperature thresholds, along with previously determined field estimates of instantaneous winter natural mortality rate (M), were used to develop models for predicting M. Historic daily water temperatures were used to estimate winter M of spotted seatrout from 1994 to 2015. Predictions of M suggest winterkill (≥50% population loss) in eight of the last 22 years; these years correspond to anecdotal and fishery-independent observations of winterkill events in North Carolina. The results of this study provide strong evidence for thermally-limited overwinter survival of spotted seatrout at its northern latitudinal limits, where winterkill events can have population-level impacts.

> "They [spotted seatrout] are so tender, that if they are in or near fresh water, and a sudden frost come, they are benumm'd, and float on the surface of the water, as if dead; and then they take up canoe-loads of them. If you put them into warm water, they presently recover."
>
> (John Lawson, A New Voyage to Carolina, 1709)

1. Introduction

Temperature has long been regarded as the dominant environmental factor governing life in aquatic ecosystems (Fry, 1947; Brett, 1956). As obligate poikilotherms, most fishes endure routine variability in their thermal environment, which can cause a cascade of controlling, directive, and lethal effects on physiology (Fry, 1971; Neill et al., 1994; Coutant, 2012). Within an optimal range, temperature controls the metabolic rates that afford energy for activity (e.g., swimming and feeding) and growth. Suboptimal temperatures direct behavior intended to reduce thermal stress and to improve chances of success or survival, such as seasonal migrations to favorable spawning or overwintering habitats. Temperature-induced mortality can be rapid and is relative to the extent to which fishes are stressed beyond thermal limits. Given that these thermal constraints on fish physiology and survival are pervasive throughout life history, temperature tolerances largely define the movement and distribution of marine species (Neill, 1979; Davenport and Slayer, 1993; Tittensor et al., 2010).

In temperate latitudes, variability in and vulnerability to abiotic factors, particularly temperature, are considered highest at the edges of a species' range and can result in strong environment-recruitment correlations (Miller et al., 1991; Myers, 1998). Furthermore, it is widely viewed that winter mortality in fishes is most severe at a species' northern boundary (Hurst, 2007). Recent reviews of low-temperature stress

* Corresponding author.
E-mail addresses: taellis@ncsu.edu (T.A. Ellis), jabuckel@ncsu.edu (J.A. Buckel), jhightower@ncsu.edu (J.E. Hightower), steve.poland@ncdenr.gov (S.J. Poland).
[1] Present address: North Carolina Division of Marine Fisheries, 3441 Arendell St., Morehead City, NC, 28557, USA.

http://dx.doi.org/10.1016/j.jembe.2017.01.010

and the propensity for that stress to become lethal suggest that despite a thorough understanding of the mechanisms driving thermally-limited overwinter survival in marine and estuarine fishes, the cold tolerance of most species is either not known or has received limited study (Hurst, 2007; Donaldson et al., 2008). The latter applies to spotted seatrout, *Cynoscion nebulosus* (Cuvier, 1830), a warm-temperate estuarine-dependent species of high economic importance to the saltwater recreational fishery in the United States. Although abundant throughout the U.S. South Atlantic and Gulf of Mexico, spotted seatrout are uncommon north of Chesapeake Bay (Bortone, 2003; ASMFC, 2011).

Arctic cold fronts periodically expose fishes, including spotted seatrout, in relatively shallow temperate estuarine ecosystems to rapid temperature declines. In the absence of thermal refugia, the main limitation being proximity to deeper water or ocean access, fish are subject to acute cold stress often resulting in mortality. Episodic mass mortalities of spotted seatrout have been attributed to harsh winter conditions across much of the species' range; hereafter, these events are referred to as winterkill (Storey and Gudger, 1936; Gunter and Hildebrand, 1951; Moore, 1976; McEachron et al., 1994; NCDMF, 2012). In Florida, air temperatures of 7 to 9 °C reportedly lowered water temperatures similarly and were lethal for spotted seatrout (Tabb, 1958); however, others have observed more directly that spotted seatrout in Florida are capable of surviving exposure to 6 °C water (Gilmore et al., 1978). In Texas, spotted seatrout mortality was observed in areas where water temperatures reached lows of 3 to 4 °C (Gunter and Hildebrand, 1951). Similarly, and from the same general geographical region, Moore (1976) reported that spotted seatrout were stressed when waters reached 7 °C and did not survive exposure to temperatures below 5 °C; however, spotted seatrout in Texas were apparently not stressed at temperatures above 10 °C (McEachron et al., 1994). These reported observations over the last half-century contribute anecdotal information on cold tolerance for spotted seatrout, which has led to an incomplete, geographically restricted, and largely speculative understanding of the thermal and other environmental conditions related to winterkill of this species.

Recent empirical studies have defined a more reliable range for cold tolerance of spotted seatrout. In an analysis of the movements and fates of telemetered fish in North Carolina, Ellis et al. (2017) provided the first direct field-based estimates of spotted seatrout survival relative to the frequency and severity of cold temperatures. Those results indicated that daily natural mortality rates (M) were elevated at temperatures below 7 °C, with a precipitous increase occurring at approximately 4 °C. Laboratory results for hatchery-reared juvenile spotted seatrout from South Carolina suggest that critical (3.6 °C) and lethal (3.1 °C) lower thermal limits are similar (Anweiler et al., 2014). Acute cold stress relative to salinity, however, has not been examined for spotted seatrout, and given that low temperatures may impede osmotic and ionic regulation, salinity has the potential to affect cold tolerance in fishes (Overstreet, 1974; Hurst, 2007; Donaldson et al., 2008). Throughout their geographical distribution, spotted seatrout reside in oligohaline to polyhaline habitats, including during winter (Wohlschlag and Wakeman, 1978; Mercer, 1984; Johnson and Seaman, 1986; NCDMF, 2012). Therefore, an analysis of the potential ancillary effects of salinity on acute cold stress is needed for a more complete understanding of the environmental conditions resulting in winterkill of this species.

An investigation of spotted seatrout mortality associated with acute cold stress is particularly relevant at the species' northern latitudinal limits where winter conditions are highly variable and there is a higher frequency of severe cold events relative to elsewhere in the species' geographic distribution. Acute cold stress of spotted seatrout has been observed for at least three centuries in North Carolina (Lawson, 1709; Smith, 1907; NCDMF, 2012) and periodic declines in the state's abundance of spotted seatrout over the last two decades were suspected to be a result of winterkill (Jensen, 2009; NCDMF, 2015). Recent mark-recapture data indicate extensive overwinter loss of spotted seatrout in the species' northern range during 2009 and 2010 (Ellis, 2014). Furthermore, in an unprecedented response to widespread reports of lethargic and moribund fish, managers in North Carolina have temporarily closed the state's recreational and commercial spotted seatrout fisheries twice in the last six years. Reducing subsequent fishing mortality of surviving adults prior to peak spawning in summer may speed recovery of the population following severe winter conditions (McEachron et al., 1994). Even so, the emergency implementation of these temporary closures was a precautionary response to perceived catastrophic winterkill, but managers lack objective criteria on which to base such restrictive regulation.

Adequate empirical data on thermal minimum limitations are fundamental to predicting the effects of winterkill on spotted seatrout population dynamics throughout the species' geographic distribution, especially in its northern range. Here, acute cold stress of spotted seatrout was examined under controlled laboratory experiments, which allowed for replication of abiotic conditions typical of North Carolina estuarine overwintering habitats and testing of the effects of low-temperature severity and salinity on survival. These empirical estimates of low-temperature thresholds were used along with previously determined estimates of M from a multiyear tag-return study (see Ellis, 2014) to develop temperature-based models for predicting winter M, which were then applied to recent water temperature data from North Carolina to predict winter M of spotted seatrout for each of the last 22 years.

2. Methods

2.1. Cold-tolerance experiments

Two common laboratory methods for exposing fish to dynamic decreases in water temperature were used to evaluate the cold tolerance of spotted seatrout as affected by temperature severity and salinity. First, stressful (but sublethal) low temperatures were determined across two representative overwinter salinity treatments using critical thermal minimum (CTMin) methodology (see review by Beitinger et al., 2000). This method precludes the reacclimation of fish to treatment temperatures, which can bias estimates of thermal tolerance (Beitinger and Bennett, 2000); however, the necessary rate of temperature change is typically faster than that observed in nature. Second, acclimated chronic exposure (ACE) methodology (e.g., Lankford and Targett, 2001; Selong et al., 2001; Carveth et al., 2007) was used to examine survival at prolonged exposure to temperatures at or just above CTMin and across the same two salinity treatments. Although fish are permitted to reacclimate to treatment temperatures with this method and a lethal endpoint is required, more natural rates of temperature decline can be experimented with, which may generate more suitable estimates of low-temperature tolerance (Beitinger et al., 2000).

Spotted seatrout ($N = 130$) were collected using hook and line from mesohaline (salinity range of 5–15; $n = 78$; 34° 55″ 09″ N, 76° 54″ 27″ W) and polyhaline (salinity range of 25–30; $n = 52$; 34° 21″ 06″ N, 77° 39″ 03″ W) habitats in North Carolina during January to March 2012 when water temperatures ranged from 11 to 15 °C. Collecting experimental fish directly from these habitats with differing saline conditions (as opposed to acclimating fish in the lab to a desired salinity) was done in case local adaptation (i.e., regional differences in cold tolerance) existed. Only fish that did not exhibit physical signs of being adversely affected by the angling process (i.e., no excessive bleeding or tissue damage) were kept as candidates for experimental use. All candidate fish were immediately placed in onboard holding tanks (at least 100 L in size) containing ambient water. Water quality was maintained through frequent water changes, continuous aeration, and supplemental oxygenation. Once the desired sample size was achieved (within 3–6 h), specimens were transported to a research laboratory in Morehead City, North Carolina and held in a 1000-L rectangular fiberglass tank with recirculated saltwater and continuous aeration. Desired salinities were achieved by adjusting sand-filtered seawater with carbon-filtered tap water. Spotted seatrout collected from mesohaline