Vol. 609: 179–186, 2019
https://doi.org/10.3354/meps12817

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 17

Flatfish utilize sediment blanket to facilitate thermoregulation

Catherine M. Ziegler[1,2,*], Michael G. Frisk[2]

[1]New York State Department of Environmental Conservation, East Setauket, New York 11733, USA
[2]School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11794-5000, USA

ABSTRACT: Animals confront thermoregulatory constraints that define species ranges, impact productivity, and limit their ability to cope with long-term environmental change. Marine poikilothermic species are assumed to have a body temperature comparable to ambient temperatures as well as possess a limited ability to behaviorally regulate body temperature. Winter flounder *Pseudopleuronectes americanus* is a migratory species with a complex life history that places it in environments that exceed the species' thermal tolerance. To determine if winter flounder use temperature refuge during seasonally cold and warm periods, we evaluated internal body temperature relative to water temperature, utilizing acoustic telemetry in a southern New England estuary. The internal body temperature of individuals commonly exceeded that of ambient water during the winter, and conversely, remained lower than ambient water during the summer. During a 3 mo trial, Kalman filter time series analysis indicated that internal body temperatures of winter flounder exhibited greater similarity to sediment temperature recorded at depths of 3, 6 and 9 cm compared to water temperature, indicating that winter flounder use burial as a strategy for thermoregulation. Such discoveries have the potential to transform our understanding of the complex interaction between environmental conditions and behavior, providing critical insight into phenomena that underpin species' life history strategies.

KEY WORDS: Behavioral strategy · Behavioral thermoregulation · Climate change · Environmental extremes · Burial · Acoustic telemetry

1. INTRODUCTION

During much of the 19th and early 20th centuries, our understanding of marine fish movement and behavior was based on oceanographic processes with the assumption that the animals were poikilothermic and had little ability to control their body temperature (Carey et al. 1971, Block et al. 1993, Frisk et al. 2014). In recent years, the discoveries of regional endotherms and a species with whole-body endothermy have provided examples of the ability of fishes to maintain body temperatures that differ from the surrounding environment (Linthicum & Carey 1972, Block et al. 1993, Graham & Dickson 2004, Bernal et al. 2005, Wegner et al. 2015). The application of modern telemetry technology is rapidly unraveling the behaviors that animals utilize to respond to environmental conditions, and is expanding our understanding of how fish process and respond to environmental conditions (Heupel et al. 2005, Welsh & Bellwood 2012, Bailey & Secor 2016).

Organisms face increased thermoregulatory challenges as a rapidly changing climate exposes individuals to temperature extremes, causing distributional shifts that, in some cases, reduce population-level productivity (Nye et al. 2009, Pinsky et al. 2013). Documenting behavioral approaches or strategies to cope with extremes is essential to understanding how species may respond to environmental change. Burial to avoid environmental extremes has been documented in some species, such as longfin dace *Agosia chrysogaster*, as a means to escape harsh environmental

*Corresponding author: catherine.ziegler@dec.ny.gov

conditions (Minckley & Barber 1971). Plains killifish *Fundulus kansae* bury in shallow streams to avoid intense sunlight and to aid in survival under drought conditions (Minckley & Klaassen 1969). However, the frequency and functionality of this behavior remains largely unexplored in most teleost taxa.

Winter flounder *Pseudopleuronectes americanus* have an unusual migratory and reproductive life history, whereby mature individuals spawn in estuarine habitats during winter and migrate offshore in spring (Lobell 1939, Perlmutter 1947). To support this strategy, winter flounder produce an antifreeze protein that acts as the fish's defense against freezing during the winter (Duman & DeVries 1974). Recently, a resident contingent of winter flounder has been observed to remain inshore during the summer when temperatures exceed the species' thermal tolerance (Sagarese & Frisk 2011, Ziegler 2017). Winter flounder not only face metabolic challenges during the winter, but summer residents also face water temperatures up to 30°C (Ziegler 2017), which far exceed their reported thermal tolerance of 19°C (Klein-MacPhee 2002). Winter flounder's life history makes it a model species to evaluate approaches that animal taxa utilize to behaviorally respond to challenging environmental conditions, such as climate change.

Burial behavior by winter flounder is hypothesized as a strategy to increase the likelihood of catching prey and avoiding predation (Ansell & Gibson 1993). However, we found evidence suggesting that winter flounder utilize the unique behavioral strategy of burial as a mechanism to maintain body temperature in extreme environmental conditions. Summer burial was observed by a diver in 1969 when sediment temperatures were lower than that of the water (Olla et al. 1969); however, to date, burial has not been identified as a thermoregulatory function in winter flounder. Here, we used passive acoustic telemetry to explore a behavioral strategy in a marine flatfish that allows the species to regulate its body temperature and provides protection from environmental extremes and variability. The use of acoustic tags with the ability to monitor temperature has provided a means to characterize fine-scale habitat use that has previously not been available to researchers. We compared internal body temperatures of telemetered winter flounder with that of ambient bottom water temperature over a 2 yr period, and with sediment temperatures at 3, 6, and 9 cm depths during a 3 mo field trial. Our main research objective was to determine if winter flounder use burial as a thermoregulatory strategy during the winter and summer months by comparing internal body temperature to water and sediment temperatures.

2. MATERIALS AND METHODS

2.1. Tagging and passive tracking of winter flounder

Mature adult winter flounder (n = 23) were captured and tagged between the months of February and March 2016 and then again in January 2017 in Mattituck Creek, NY (40.99° N, 72.54° W). Upon capture, total length for each individual was measured to the nearest mm. Adults greater than 240 mm were equipped with an acoustic transmitter (Model V9T-2L, VEMCO; 69 kHz, 9 × 44 mm, accuracy: ±0.5°C from −5 to 40°C) to measure internal body temperature and provide location. Each tag was surgically implanted into the peritoneal cavity following Stony Brook University's Institutional Animal Care and Use Committee approved protocols (IACUC #702275). The tag was programmed to ping randomly every 80–160 s, with an estimated battery life of 679 d. Once implanted with the transmitter, the fish was placed in a holding tank to recover. After the individual resumed normal behavior, it was immediately released at the site of capture. Each individual resumed normal behavior within 5 min of being placed in the holding tank.

A total of 11 acoustic transceivers (VEMCO; diameter: 308 × 73 mm) were mounted on concrete blocks or attached to pilings and placed throughout the inlet and creek (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m609p179_supp.pdf). Each receiver was placed approximately 500 m apart based on the approximate detection radius for the region and similar habitat (Divver 2012, McCauley et al. 2014). The receivers were placed in the creek so their detection radius would not overlap, except for the double gate by the inlet. However, due to the depth of the creek and other circumstances out of our control, the detection radius of some receivers, such as receivers 7 and 8, did slightly overlap (Fig. S1). When a telemetered fish was within range of the transceiver, the internal body temperature of the fish, the transmitter's ID, and the date and time were recorded. Water temperature was measured every 3 h by all transceivers (Model VR2Tx, VEMCO; accuracy: ±0.5°C from −5 to 40°C).

Two field components were analyzed: (1) a comparison between environmental water temperature and long-term internal temperature tags that were deployed over 2 yr, and (2) a 3 mo field trial when internal temperature tags were deployed simultaneously with measurements of water and sediment temperatures. Data analyses for both components of the project were similar and are presented together unless noted otherwise.

2.2. Long-term behavior

The difference between the internal body temperature of the fish and the water temperature was calculated for all individuals. The mean difference between the internal body and water temperature per day for all fish was calculated and presented as a monthly average. This was achieved by calculating the daily average difference between internal body and water temperature for all monitored individuals and averaging those values for each month. Similarly, the mean of the maximum difference between internal body and water temperature was calculated by averaging the daily maximum difference for all monitored individuals and averaging those values for each month. To determine the possible extent of the temperature difference obtainable, we took the maximum difference observed by any of the telemetered individuals per day. Thus, the daily maximum difference was the maximum difference observed per day across all individuals and averaged for the month. Differences were only calculated when a tag detection occurred. This approach treats daily averages as independent estimates. Additionally, the number of telemetered individuals present varied over the study; thus, the number of observations varied by month (see Fig. 1). These analyses are intended to provide overall seasonal trends in the difference between internal body temperature and water temperature. Error was assessed by the standard error of the mean for each month. The percentage of detections where the difference between internal body and water temperature was greater than 1, 2 and 3°C were calculated to measure the extent of winter flounder thermoregulation.

The locations of the telemetered individuals in the creek were plotted against the internal body and water temperatures to observe temperature trends over time in relation to movement. Periods where the internal body and water temperature cycles matched in amplitude, and to a lesser extent frequency, were assigned as non-burial periods. Periods where the internal body and water temperature cycles matched in frequency, but the amplitude differed were assigned as burial periods. A previous field test was performed to determine the performance of VEMCO acoustic tags at various depths in Long Island habitat (C. Martinez, K. Dunton & M. Frisk pers. obs.). The field test indicated that at 30.4 m away from the receiver, transmitters that were buried 3 and 6 cm were detected, but at a lower probability than transmitters at the surface. Thus, the telemetered individuals detected were located near the receiver with water and internal body temperatures paired at the time of detection.

2.3. Field trial sediment comparison

Sediment temperature was measured in Mattituck Creek for approximately 3 mo. Temperature and light loggers (Model UA-002-64, HOBO Pendant; accuracy: ±0.53°C from 0 to 50°C) were mounted to 3.2 cm diameter PVC pipes which were cemented into a mooring. A total of 10 moorings, each with 3 temperature and light loggers, were attached to 3 separate PVC pipes and inserted into the sediment by a diver. Loggers were positioned in the sediment at depths of 3, 6, and 9 cm. Temperature was measured every 30 min. Locations of these devices in the creek were chosen to represent areas preferred by winter flounder based on the highest detections for this time period (Ziegler 2017).

A Kalman filter was used to calculate 95% confidence intervals for time series of internal body, water, and sediment temperatures using the NOAA Fisheries Toolbox. The Kalman filter is composed of (1) an observation and (2) a state equation:

$$y_t = q_t b_t + v_t \quad (1)$$

$$b_t = b_{t-1} + w_t \quad (2)$$

where y_t is the observation vector and b_t is the state vector and v_t and w_t represent normal errors with a mean of zero (Meinhold & Singpurwalla 1983, Durbin & Koopman 2001). The NOAA Fisheries Toolbox requires a vector of observations (y_t), observation error represented as the coefficient of variation for each of the t periods, and a scale vector (q_t), which we chose to be 1. The Kalman filter algorithm works recursively to update the state given the observations over time, and uses maximum likelihood to estimate b_0 and standard error of the state variable (Durbin & Koopman 2001). The model produces filtered and smoothed observations with 95% confidence intervals that can be used to compare the time series.

Internal body temperature was recorded when fish were within the detection range of a transceiver. Thus, average internal body temperature was grouped every 12 h to provide a time series that was less affected by the tidal cycles and had an adequate number of detections per time interval. If there was a period of 12 h where a fish was not detected by a transceiver, and therefore no internal body temperature was recorded for that period, the average of the 12 h period prior and after was used. If there was more than one continuous 12 h period where the fish was not detected, i.e. a day or longer, that period was not used in the Kalman filter estimation. Average water temperature for the Kalman filter was taken from a centrally located receiver in a region of high abundance of telemetered individuals.

3. RESULTS

3.1. Long-term behavior

The mean internal temperature of the telemetered individuals was warmer than the water temperature during the winter and cooler than the water temperature during the summer (Fig. 1). For all months, both the mean difference and the maximum mean difference followed the same trend among individuals; i.e. either both values were positive or both values were negative. Over the duration of the project, all telemetered winter flounder experienced a difference between internal body and water temperature of 1°C or greater (Table 1). The difference between internal body and water temperature varied greatly between individuals and time (Table 1). The daily maximum difference was greater by more than 1°C for some months, indicating the extent of possible behavioral thermal regulation.

Individuals exhibited large differences between internal body and water temperature when they were not moving between receivers, as shown by the overlying trends in internal body and water temperatures (Fig. 2, Fig. S2 in the Supplement). For example, the individual depicted in Fig. 2 remained near receiver 9 (as shown by the steady black line at

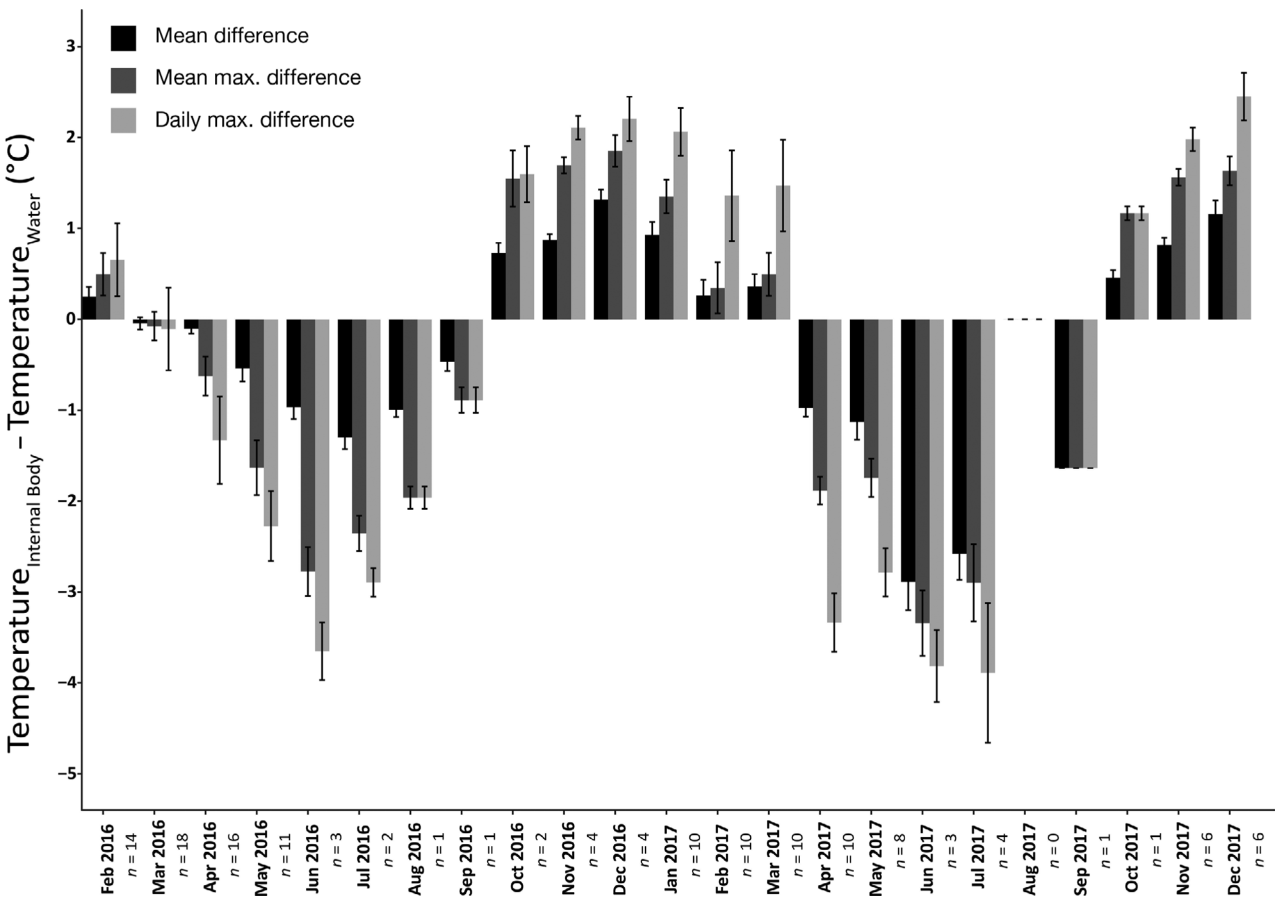

Fig. 1. Temperature difference per month for telemetered winter flounder showing mean (±SE) difference between internal body and water temperatures, mean maximum difference, and daily maximum difference. Sample size during each month is indicated under the date on the *x*-axis. Sample size corresponds to the number of fish present in the creek during each month and therefore the number of fish that were in each month's calculation. Positive values indicate that the fish's internal body temperature was higher than the water temperature; negative values indicate that the fish's internal body temperature was lower than the water temperature

Table 1. Differences between internal body temperature and water temperature of telemetered winter flounder. Average difference was calculated by subtracting the water temperature from the internal body temperature and then averaging across all detections of the individual fish. Columns 4–6 represent the percent of detections that resulted in a difference between internal body and water temperature greater than 1, 2, and 3°C

Tag no.	Avg. diff	Max. diff	>1°C (%)	>2°C (%)	>3°C (%)	No. of days in creek
46	0.23 ± 0.003	3.30	25.81	3.96	0.14	236
47	0.10 ± 0.007	3.20	18.05	1.08	0.15	93
48	0.08 ± 0.007	4.13	22.83	2.28	0.37	81
50	0.56 ± 0.002	4.41	15.23	1.71	0.33	345
51	0.26 ± 0.005	4.14	28.02	2.42	0.48	98
53	0.51 ± 0.018	1.93	7.99	0.00	0.00	10
54	0.26 ± 0.015	3.98	26.54	5.51	2.04	60
55	−0.07 ± 0.004	4.10	36.89	8.83	2.28	226
56	−0.67 ± 0.010	4.29	36.60	9.54	0.72	55
58	−0.02 ± 0.006	4.45	33.19	6.88	0.76	73
59	−0.34 ± 0.006	3.82	23.55	4.28	1.29	72
60	−0.20 ± 0.013	3.20	23.46	3.21	0.24	22
61	−0.28 ± 0.008	7.17	69.13	33.36	14.01	435
62	−0.05 ± 0.007	4.29	27.39	4.74	1.58	72
63	0.03 ± 0.003	4.13	25.24	3.30	0.34	186
64	−0.60 ± 0.010	3.98	35.15	6.94	1.13	58
65	0.03 ± 0.008	3.98	25.31	3.94	0.85	55
66	0.30 ± 0.006	3.67	28.75	3.02	0.70	71
73	−0.31 ± 0.006	3.77	16.54	2.32	0.03	138
74	−0.39 ± 0.012	6.01	52.98	18.39	5.24	154
75	−0.05 ± 0.006	3.42	25.14	2.44	0.24	106
76	−0.22 ± 0.008	5.54	37.03	8.94	1.98	138
77	−0.51 ± 0.009	5.69	40.95	11.91	3.60	128

receiver 9) until beginning movement toward the inlet, when it was detected on receivers 1–4, moving towards the Long Island Sound (Fig. 2). Once the individual started to move (approximately 23 April 2016), the value, trend, and amplitude of internal temperature closely matched that of the water temperature (Fig. 2).

3.2. Field-trial sediment comparison

A Kalman filter was used to obtain 95% confidence intervals to compare internal body, water, and sediment temperatures (n = 10). This revealed that all individuals displayed differences between internal body and water temperature at some point during the 3 mo experiment (Fig. 3 & Fig. S3 in the Supplement). Throughout periods when internal body temperature deviated from water temperature, internal body temperature more closely matched sediment temperature, indicating burial (Figs. 3 & S3). The greatest difference be-

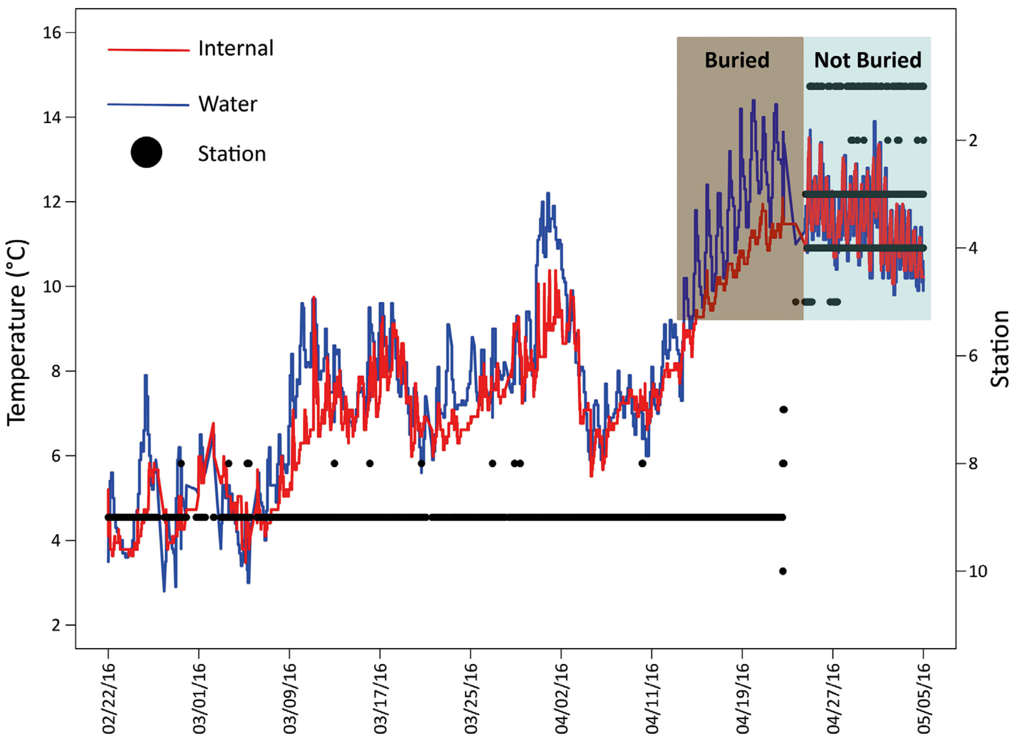

Fig. 2. Time series of internal body temperature of an individual winter flounder measured by acoustic temperature tags compared to bottom water temperature measured at the receiver. Black dots: receiver detections at the stations within Mattituck Creek; brown boxed area: period when the telemetered individual is assumed to be buried (body < water temperature); light blue boxed area: period when the individual is assumed to be actively swimming (body ≈ water temperature) and moved from receiver 9 towards the inlet and between receivers 1–4. See Fig. S2 in the Supplement for additional telemetered winter flounder

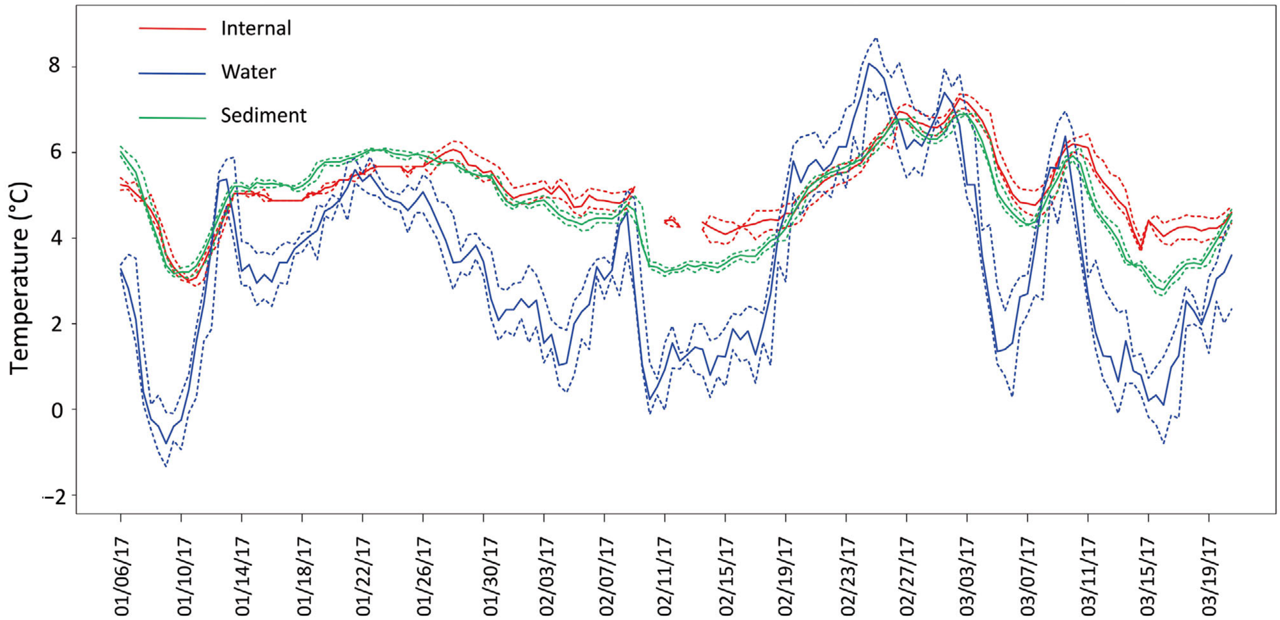

Fig. 3. Time series from the Kalman filter of the 3 mo field trial. Solid lines: internal body, water, and sediment measured temperature values; dashed lines: the 95th and 5th confidence percentiles for each respective temperature. See Fig. S3 in the Supplement for an additional 3 examples

tween the internal body and water temperature for all 10 fish occurred when water temperatures were coldest; all differences occurred at water temperatures of 4°C or below (Figs. 3 & S3). Internal body and sediment temperatures overlapped for all 10 fish, while there were only a few periods when internal body and water temperature overlapped (Figs. 3 & S3).

4. DISCUSSION

We documented a unique behavioral strategy to regulate internal body temperature that has broad applications to understanding how species cope with extreme environments and climate change. Our research presents the discovery that winter flounder bury to find temperature refuge during the winter and summer months when water temperature is out of the species' thermal tolerance range. This discovery is of significance, as poikilothermic animals are assumed to have little ability to regulate temperature. Here, we showed that behavior can be utilized to achieve a difference in body and ambient water temperature as high as that achieved by the recent discovery of the endothermic opah *Lampris guttatus* (Wegner et al. 2015).

Behavioral tactics are a common approach to optimize energy use and thus increase fitness (Smith 1978, Bernatchez & Dodson 1987). Further, residing in areas with cool or warm water, depending on the season, can allow fish to conserve energy for growth and reproduction in addition to basal metabolic processes (Berman & Quinn 1991). Studies on a wide variety of teleost species have revealed that body temperatures are usually within 1°C of the water temperature (Carey et al. 1971, Linthicum & Carey 1972). Over the duration of this study, all telemetered winter flounder experienced a difference between internal body and water temperature >1°C, with a single individual experiencing a difference >3°C for 14% of its detections and maximum difference of 7.2°C.

During the winter spawning period (January–March), the mean maximum difference is an appropriate metric of temperature buffering due to burial, as during active movement the internal body temperature will remain within 1°C of water temperature for poikilothermic fishes (Carey et al. 1971, Linthicum & Carey 1972). During spawning, fish are likely to change behavior with a greater frequency, i.e. shifting from buried to unburied. Seasonal patterns in temperature suggested that winter flounder were selecting warmer habitat in the winter and cooler in the summer through burial. A stronger trend is observed when the mean maximum difference between internal body and water temperature is considered. Not all individuals followed the overall trend in temperature regulation, but instead displayed variation in the seasonal timing of burial to select cooler/

warmer environments, especially during periods of transition between seasons.

The time series of internal body temperature of individual winter flounder and water temperature matches the expectation that fish bury, and differences were more evident when fish were not moving between transceivers. An abrupt shift from disparate to matching temperature and frequency trends provides an indicator that the individual was buried, then began moving towards the inlet, eventually migrating out of the creek. These findings are consistent with previous observations by Olla et al. (1969) that winter flounder bury in the summer months when the water temperature reached 23°C, and Grothues et al. (2012), who found that not only do winter flounder also bury in the winter, but they bury deeper as temperatures decrease. Additionally, it is unknown whether the physiological demands from spawning impact the need to thermal regulate during the winter to maximize spawning and recovery.

Our evidence suggests that temperature extremes, whether warm or cold, drive behavioral responses in winter flounder, especially as temperatures approach lethal values of −1.4°C (Duman & DeVries 1974) and 19.3°C (Klein-MacPhee 2002). During the field trial, on average, winter flounder buried between temperatures of 1.45 and 4.45°C. The Kalman filter could not be performed during the summer months when the water temperature was the warmest, due to gaps in the acoustic data. The gaps in the data did not have an associated movement out of the creek and began when the water temperature was between 20 and 24°C. During these gaps, individuals were most likely buried too deep to be detected, suggesting the possibility of larger differences between water and internal body temperatures. These long gaps in the acoustic data are during periods of increasing water temperature and during the warmest temperatures recorded, suggesting we may be underestimating the full extent to which this species utilizes burial for thermoregulation. Future research that improves the detection of buried individuals and associated body temperatures will likely reveal greater potential to thermoregulate.

Laboratory studies showed that winter flounder adjust to short-term environmental warming by increasing their oxygen consumption at higher temperatures, while keeping their cardiac output constant (Cech et al. 1976, Mendonça & Gamperl 2010). Our study implies that winter flounder bury deep into the sediment to thermoregulate. To our knowledge, this is one of the first studies documenting this behavior for this purpose, and therefore information such as their ability to obtain oxygen while buried remains unknown. Future research addressing metabolic effects/benefits of burial behavior is an important next step to identify how winter flounder cope with extreme temperatures and perhaps long-term changes in climate.

The water temperature of the creek at any given time was relatively uniform throughout the study period, suggesting that individuals had little ability to find refuge by moving throughout the creek (Fig. S4 in the Supplement). Further, all buried individuals remained near receivers 8 and 9 and did not move to the inlet or into the fingers of the system, where slightly different temperatures could be located. We are confident we did not miss movements towards the inlet during the study, as receivers had high probabilities of detecting migration in and out of the creek (Ziegler 2017). Since the general area of burial was determined in the current project, future research that increases the number of water and sediment measurements would provide higher resolution of the thermal regulatory potential of burial and increase our understanding of this phenomenon.

Over the last decade, advances in telemetry technology have allowed the observation of fine-scale behaviors of fishes that previously eluded researchers, and are just beginning to reveal the diversity of behaviors utilized by species to respond to complex environments (Welsh & Bellwood 2012, Bailey & Secor 2016). A greater understanding of the interaction between the environment and behavior has the potential to revolutionize our understanding of fish habitat preferences and utilization. Here, we documented burial in winter flounder, but it is unknown whether other flatfish, and other teleost species, utilize burial as a method of thermal regulation. Regardless of whether burial is unique to winter flounder, or a more common behavior in finfish, it highlights the diversity of adaptations that are likely displayed by taxa and are presently undocumented. Understanding the behaviors exhibited by species to cope with temperature is critical for understanding their ability to respond to long-term drivers such as climate change.

Acknowledgements. This project was made possible by funding from the Army Corps of Engineers and Tetra Tech. We thank Robert Cerrato and Janet Nye for their input on the research, Jill Olin and Matthew Siskey for their comments on the manuscript, and Oliver Shipley for his comments and help with the figures. We also thank Joshua Zacharias for his assistance with field sampling and Bill Pfeiffer for diving. We greatly appreciate the assistance of Captains Christian Harter, Jason Schweitzer, and David Bowman, as well as Strong's Marina.

LITERATURE CITED

Ansell AD, Gibson RN (1993) The effect of sand and light on predation of juvenile plaice, *Pleuronectes platessa*, by fishes and crustaceans. J Fish Biol 43:837–845

Bailey H, Secor DH (2016) Coastal evacuations by fish during extreme weather events. Sci Rep 6:30280

Berman CH, Quinn TP (1991) Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. J Fish Biol 39:301–312

Bernal D, Donley JM, Shadwick RE, Syme DA (2005) Mammal-like muscles power swimming in a cold-water shark. Nature 437:1349–1352

Bernatchez L, Dodson JJ (1987) Relationship between bioenergetics and behavior in anadromous fish migrations. Can J Fish Aquat Sci 44:399–407

Block BA, Finnerty JR, Stewart AFR, Kidd J (1993) Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. Science 260:210–214

Carey FG, Teal JM, Kanwisher JW, Lawson KD, Beckett JS (1971) Warm-bodied fish. Am Zool 11:137–143

Cech JJ Jr, Bridges DW, Rowell DM, Balzer PJ (1976) Cardiovascular responses of winter flounder, *Pseudopleuronectes americanus* (Walbaum), to acute temperature increase. Can J Zool 54:1383–1388

Divver MM (2012) Examining the ecological role of white perch (*Morone americana*) using acoustic telemetry in the Great South Bay Estuary, New York. MSc thesis, State University of New York, Stony Brook, NY

Duman JG, DeVries AL (1974) Freezing resistance in winter flounder *Pseudopleuronectes americanus*. Nature 247: 237–238

Durbin J, Koopman SJ (2001) Th Kalman filter. In: Time series analysis by state space methods. Oxford University Press, New York, NY, p 11–13

Frisk MG, Jordaan A, Miller TJ (2014) Moving beyond the current paradigm in marine population connectivity: Are adults the missing link? Fish Fish 15:242–254

Graham JB, Dickson KA (2004) Tuna comparative physiology. J Exp Biol 207:4015–4024

Grothues TM, Able KW, Pravatiner JH (2012) Winter flounder (*Pseudopleuronectes americanus* Walbaum) burial in estuaries: acoustic telemetry triumph and tribulation. J Exp Mar Biol Ecol 438:125–136

Heupel MR, Simpfendorfer CA, Lowe C (2005) Passive acoustic telemetry technology: current applications and future directions. Mote technical report no. 1066. Mote Marine Laboratory, Sarasota, FL

Klein-MacPhee G (2002) Winter flounder (*Pseudopleuronectes americanus*) (Walbaum 1792). In: Collette BB, Klein-MacPhee G (eds) Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edn. Smithsonian Institution Press, Washington, DC, p 560–587

Linthicum DS, Carey FG (1972) Regulation of brain and eye temperatures by the bluefin tuna. Comp Biochem Physiol A 43:425–433

Lobell MJ (1939) A biological survey of the salt waters of Long Island, 1938. Report on certain fishes. Winter flounder (*Pseudopleuronectes americanus*). In: Supplement to the 28th annual report, part 1. New York State Conservation Department, Albany, NY, p 63–90

McCauley MM, Cerrato RM, Sclafani M, Frisk MG (2014) Diel behavior in white perch revealed using acoustic telemetry. Trans Am Fish Soc 143:1330–1340

Meinhold RJ, Singpurwalla ND (1983) Understanding the Kalman filter. Am Stat 37:123–127

Mendonça PC, Gamperl AK (2010) The effects of acute changes in temperature and oxygen availability on cardiac performance in winter flounder (*Pseudopleuronectes americanus*). Comp Biochem Physiol A Mol Integr Physiol 155:245–252

Minckley W, Barber W (1971) Some aspects of biology of the longfin dace, a cyprinid fish characteristic of streams in the Sonoran Desert. Southwest Nat 15:459–464

Minckley CO, Klaassen HE (1969) Burying behavior of the plains killifish, *Fundulus kansae*. Copeia 1969:200–201

Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar Ecol Prog Ser 393:111–129

Olla BL, Wicklund R, Wilk S (1969) Behavior of winter flounder in a natural habitat. Trans Am Fish Soc 98:717–720

Perlmutter A (1947) The blackback flounder and its fishery in New England and New York. Bull Bingham Oceanogr Collect Yale Univ 11:1–92

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. Science 341:1239–1242

Sagarese SR, Frisk MG (2011) Movement patterns and residence of adult winter flounder within a Long Island estuary. Mar Coast Fish 3:295–306

Smith JM (1978) Optimization theory in evolution. Annu Rev Ecol Syst 9:31–56

Wegner NC, Snodgrass OE, Dewar H, Hyde JR (2015) Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. Science 348:786–789

Welsh JQ, Bellwood DR (2012) Regional endothermy in a coral reef fish? PLOS ONE 7:e33187

Ziegler CM (2017) Migration diversity, spawning behavior, and temperature selection of winter flounder. MSc thesis, State University of New York, Stony Brook, NY

Editorial responsibility: Jana Davis, Annapolis, Maryland, USA

Submitted: June 12, 2018; Accepted: November 5, 2018
Proofs received from author(s): December 18, 2018