THE EFFECT OS SALINITY AND PHOTOPERIOD ON THE DIEL ACTIVITY PATTERN OF MUMMIICHOGS (*FUNDULUS HETEROCLITUS)*

by

Emil Jason Senathirajah

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Bachelor of Science with Honours in Marine Biology

Supervisor: Ben Speers-Roesch, Ph. D., Department of Biological Sciences

THE UNIVERSITY OF NEW BRUNSWICK

SAINT JOHN

April 2020

ABSTRACT

The diel cycle of activity varies among fishes. Some species show nocturnal activity, while others are diurnal or crepuscular. The diel period where fish are most active has important relationships to the species' niche and life history. Mummichogs (*Fundulus heteroclitus)* are ecologically important yet their diel cycle patterns are not well understood. Some studies report a diurnal pattern while others report a nocturnal pattern. To resolve this discrepancy, and better understand influences on the diel activity cycles of mummichogs, I investigated the effect of photoperiod and salinity on the day and night activity levels of mummichog. Mummichogs were acclimated to sea water (35ppt) or half-strength sea water, (17ppt) and their diel activity was measured after acclimation to winter (10L:14D) photoperiod and again after acclimation to summer photoperiod (12L:12D). Salinity and photoperiod had no significant effect on the diel activity pattern of mummichogs. Mummichogs maintain similar activity levels at all times.

ACKNOWLEDGEMENTS

A huge thank you to my supervisor, Dr. Ben Speers-Roesch and Connor Reeve for your constant support and guidance throughout my experiment, they were greatly appreciated. Your guidance has taught me so much about working in science and has motivated me to keep pursing in the field. I will never forget the advice you have given me and will continue to apply them to my future career.

I also want to thank my fellow honours students who have given me with feedback in various parts of the course.

STATEMENT OF RESEARCH CONTRIBUTION

The experiment was designed by Dr. Ben Speers-Roesch and Connor Reeve. I conducted the experiment, which included daily feeding and checkups on the fish, all experimental measurements of fish activity, all analysis of videos, statistical analysis of data, and write-up of the report. The recording of fish activity was done during the fall semester of 2019, while analysis of video, statistical analysis of data and thesis write-up was done during the winter 2020 semester.

Table of Contents

List of Figures

Introduction

A diel activity cycle is the pattern of activity an animal shows over a 24-hour period (Reebs, 2002). These patterns of activity can be described as diurnal (where the animal is more active during the day), nocturnal (where the animal is more active during the night), or crepuscular (where the animal is most active during dawn and dusk). The time of day where fish are more active plays an important role in their life traits such as growth, survivorship and reproductive success (Sikkel, 2014, Anderson et al., 1995, Levin, 1994). Fish species typically show consistency in these activity patterns. Some species of fish are diurnal while others are nocturnal. In many fish species, however, individuals can switch from a diurnal cycle to a more nocturnal cycle within a few days. Due to this, activity patterns of fish are thought to be plastic (Reebs, 2002). There are many abiotic factors that can influence the diel activity patterns and their plasticity.

Water temperature is one of the most important factors that affects the performance of fishes, including growth, reproduction, and activity levels (Thompson, 2019). Yet the effect of temperature on their diel cycles has received less attention (Valdimarsson et al., 1997). Because most fish are ectotherms, their body temperature matches that of the external environment. In general, fish become less active as temperature falls and physiological rates slow, and more active with warming (Valdimarsson et al., 1997). For example, Sea raven (*Hemitripterus americanus)* were observed to show an increased activity and other rate functions with increasing temperatures (Reynolds and Casterlin, 1982). Temperature can be influenced by the amount of sunlight (e.g. night can be colder than the day, and winter is much colder than summer). Studies have shown that seasonal behavioral changes occur in certain fish species. For example, Atlantic salmon (*Salmo salar L.*) are found to be more active foraging during the day in the summer rather than the winter where they are less active since they are seeking shelter (Valdimarsson et al., 1997).

The inflow of freshwater and tidal movement affects the salinity levels in coastal environments (Sakabe and Lyle, 2010a). Salinity is known to be an important factor in influencing the distribution and movement of fish (Sakabe and Lyle, 2010a). Due to the metabolic cost of ion regulation, it is assumed that fish tend to minimize this cost by behaviorally selecting intermediate salinities near the isosmotic/isoionic point (Marshall et al., 2016). Estuaries in the northern extremes tend to freeze in winter, forcing the resident mummichogs (*Fundulus heteroclitus*) to retreat to higher salinity depths in winter. With the thaw in spring, the fish return to shallow ponds (Marshall et al., 2016). Fish species have shown different levels of swimming performance with different levels of salinity (Yetsko and Sancho, 2015). For example, the Striped killifish (*Fundulus majalis)* showed significantly higher swimming performance in high salinity water than in low salinity waters (Yetsko and Sancho, 2015). Certain species of fish have shown extensive movements that is linked to tidal cycles (Sakabe et al., 2010). For example, the southern black bream (*Acanthopagrus butcheri*) have shown small-scale upstream movements during incoming tides and downstream movements during out going tides (Sakabe et al., 2010). The spotted grunter *(Pomadasys commersonnii*), an estuarine species, move upstream during incoming tides and downstream during outgoing tides, indicating that changes in tides and subsequently changes in salinity can cause changes in the movement in fish, especially estuarine species (Childs et al., 2008). Using the changes in both tides and salinity fish are able to shift their activity levels, as foraging is related to salinity/tidal shifts. Fish in general are more active during tidal movements to find better suitable habitats, and salinity could be one cue that drives such activity.

Light in the environment is highly variable and can change over a large range. The 'quality' (the different wavelengths that are absorbed by water), the 'quantity' (different intensities), and the 'periodicity' (i.e. photoperiod: daily cycle of light and dark) of light can vary seasonally depending on latitude (Boeuf and Le Bail, 1999). Photoperiod is an important factor that influences the growth, metabolic rate, and locomotor activity in many teleost fish (Biswas and Takeuchi, 2002; Boeuf and Le Bail, 1999; El-Sayed and Kawanna, 2004; Veras et al., 2013). It is also an important factor in influencing the feeding strategies in fish (Veras et al., 2013). In many species of fish, feeding is tightly coupled with their daily cycle of activity. Specifically, diurnal fish tend to be more active and feed during the day than at night, while the opposite is true for nocturnal fish. For certain species of fish, longer photoperiod can indirectly modify their growth which increases their food intake and the development of increased muscle mass by increasing their locomotor activity (Veras et al., 2013). Studies have shown that fish who are subjected to a photoperiod with more hours of light than dark had an increase activity level (Veras et al., 2013). These patterns can also change with gradual seasonal shifts in photoperiod. For example, Brown trout (*Salmo trutta*) have shown that seasonal variation in their diel activity patterns shifted progressively from a more crepuscular activity in autumn and winter to a more homogenous and intensive activity during spring and summer (Ovidio et al., 2002).

Estuaries are one of the most variable habitats due to dynamic changes in water temperature, light levels, and salinity on daily to seasonal time scales (Sakabe and Lyle, 2010a). Environmental variability in estuaries can influence fish species living there to move throughout the habitat to find more suitable conditions (Thompson, 2019). Thus, estuarine fish species are useful models to investigate the influence of environmental factors on diel activity patterns. The mummichog (*Fundulus heteroclitus)* is a model species in ecotoxicology (Schartl, 2014), embryology, physiology (Burnett et al., 2007), and evolutionary biology, especially in studies of adaptive physiological and behavioral responses to environmental change (Marshall et al., 2016; Schulte, 2007). They are a highly abundant species found in estuaries ranging from southwest Newfoundland to northern Florida (Able and Fahay, 2010). Mummichogs are one of the most important prey and food sources for many other estuarine species, so understanding their responses to different environmental conditions can help us better predict the resilience of estuarine food webs, especially when we are facing climate change (Thompson, 2019). Despite the mummichog's importance, little is known about their diel activity pattern and the factors influencing it. In fact, there is conflicting evidence as to the type of diel activity cycle they have: certain studies have indicated a diurnal pattern (Clark et al., 2003; Kavaliers, 1980) while others have shown a nocturnal pattern (Reeve and Speers-Roesch, Unpublished). An important difference between these previous studies, however, were the acclimation conditions for salinity and photoperiod. In the study that showed a nocturnal pattern (Reeve and Speers-Roesch, unpublished)**,** the mummichogs were acclimated to a winter (10L:14D) photoperiod with full strength sea water (35ppt). On the other hand, in the study showing a diurnal pattern, mummichogs were acclimated to a summer (12L:12D) photoperiod with half strength sea water (17ppt). Thus, the difference in diel pattern between these studies could be due to the different photoperiod and salinity conditions the mummichogs were acclimated to.

The aim of my study was to investigate the influence of salinity and photoperiod on the diel activity cycle of mummichogs. I hypothesize that salinity and/or photoperiod affects the diel cycle activity of mummichogs. This hypothesis was tested by measuring activity levels in mummichogs acclimated to either full strength (35ppt) or half strength (17ppt) sea water and acclimated to a winter (10L:14D) and then a summer (12L:12D) photoperiod. If my hypothesis is supported, then acclimation to half strength sea water and/or a summer photoperiod will cause mummichogs to shift to a diurnal pattern. This study will help elucidate the effects of salinity and photoperiod on the diel cycle activity of mummichogs, which has implication on their foraging, growth, survivorship and reproductive success. It will also allow us to better predict the resilience of estuarine food webs in the face of climate change.

Methods

Study organism and tagging of fish

Mummichogs of both sexes were collected using minnow traps from Sam Orr Pond, Bocabec, New Brunswick (45°09'34.7"N 67°02'36.4"W) during the summer of 2018. The fish were transferred to holding tanks at the University of New Brunswick, Saint John, supplied with recirculating filtered sea water (35 ppt) at a temperature of 14°C and acclimated to a winter (10L:14L) photoperiod. The mummichogs were fed every second day with commercial salmon pellets (Skretting Gemma, 1.8 mm).

Thirty mummichogs (with an average weight of 6.10g ± 0.76 g) were divided into groups of five (six groups of five) where four of the five fish in each group were given a specific tag in the head region to allow for individual identification. Individual fish were placed inside a Ziploc bag which was filled halfway with full strength sea water (35ppt) and a subdermal elastomer tag implanted in specific locations on the head. Fish five from each group were not given a tag but the same procedure was taken to control for stress level.

Acclimation and experimental set up

Two acclimation systems were used, each consisting of three aquaria (16 gallons) with five fish in each (15 fish in each system), supplied with recirculating filtered sea water at a temperature of 14°C but with different salinity levels (35 and 17 ppt; full strength and half-strength seawater, respectively) in the two systems. Each of the aquaria had a PVC pipe (white, 1-inch diameter, 15 cm long) for shelter. All 30 mummichogs in the two systems were first acclimated to a winter (10L:14D) photoperiod for at least four weeks and dry pallets were fed daily at 12:30pm. The temperature and the salinity levels were recorded daily, and water changes were also performed once a week to ensure ammonia level were low and to ensure the desired temperature and salinity were maintained.

After the acclimation period at 35 or 17 ppt and a winter photoperiod, 15 fish from the 35 ppt system were transferred into individual arenas (18.5 x 15 cm polypropylene containers) with a PVC pipe (3.5 x 9 cm) in each (15 arenas total) for sheltering. The individual arenas had recirculating sea water at 14°C and salinity level of 35 ppt and with the same winter (10L:14D) photoperiod. Two infrared cameras were mounted above the 15 arenas with infrared lamps to record fish activity levels during night and day. The 15 fish were given one day of acclimation and two days (i.e. two day-night cycles) of recording their individual activity levels. During this time, the fish were not fed but the temperature and the salinity levels were recorded. After recording, the fish were transferred back into their home aquaria within their acclimation system. This protocol for measuring individual activities was then repeated for the fish from the 17 ppt acclimation system.

Once the 17ppt-acclimated fish were returned to their acclimation system, all fish in the two systems were then acclimated to a summer (12L:12D) photoperiod for four weeks with the same two salinity levels maintained for each system (35 and 17ppt) at 14°C. The fish were fed daily with the same dry pellets with the temperature and the salinity levels recorded. After the four weeks of acclimation, the same method described above was used to record their individual activity levels again under summer photoperiod and their respective acclimation salinity.

Statistical analysis

The recorded videos were analyzed using an automated tracking software (ToxTrac, version 2.84, Rodriguez *et* al., 2018), which allowed us to calculate the average speed of each fish during the trials. The average speed of each fish was then divided by its respective body length to calculate spontaneous activity of each fish in body length/min (BL/min). Statistical analysis was conducted using R v.3.4.3 for statistical computing, with the α set at 0.05. A linear mixed model was performed to determine the significance of activity levels between day/night, the two photoperiods and the salinity level.

Results

Diel activity pattern under a winter photoperiod at 35ppt and 17ppt

Mummichogs showed similar spontaneous activity during day and night in both 35 and 17 ppt acclimated groups after acclimation to a winter photoperiod (Figure 1 A, C). In other words, there was no significant difference in spontaneous activity between day and night ($p=0.9853$), nor an effect of salinity ($p=0.5157$). There was no significant interaction ($p=0.9859$).

Diel activity pattern under a summer photoperiod at 35ppt and 17ppt

Mummichogs acclimated to a summer photoperiod and 35 ppt or 17 ppt both appeared to have higher spontaneous activity during the night compared to the day (Figure 1 B, D), but this was not significant. Spontaneous activity of summer photoperiod fish was not significantly different between day and night ($p=0.9215$), nor was it affected by salinity ($p=0.2682$), and there was no interaction ($p=0.3284$).

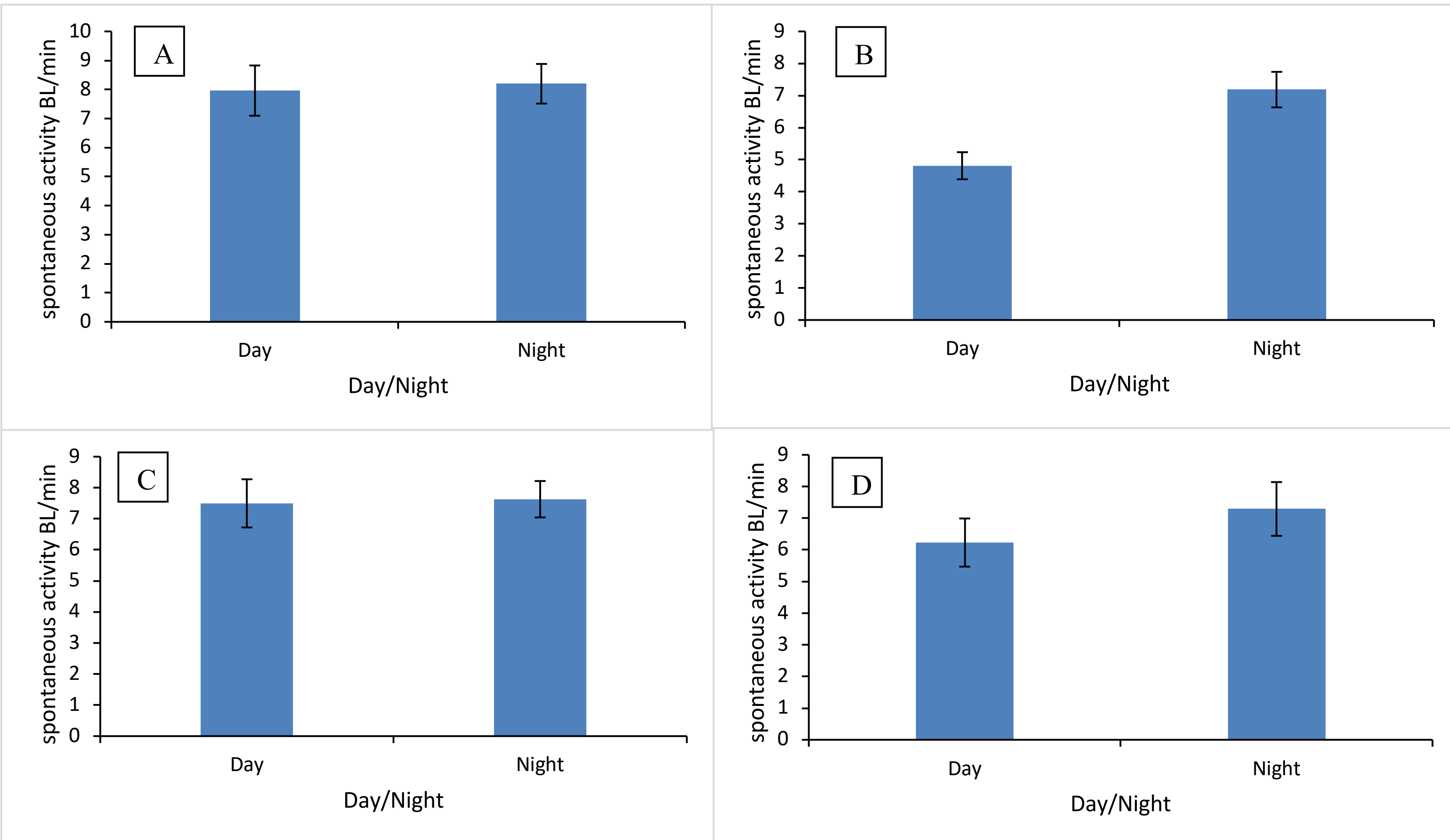

Figure 1: The average spontaneous activity during day and night of 35 ppt-acclimated mummichogs acclimated to (A) a winter (10L:14D) photoperiod, and then (B) a summer (12L:12D) photoperiod; and 17 ppt acclimated mummichogs acclimated to (C) a winter (10L:14D) photoperiod, and then (D) a summer (12L:12D) photoperiod. The data is presented as means +/- standard error of the BL/min, n=15.

Discussion

My findings showed that mummichogs exhibit similar activity during day and night and that their activity is unaffected by exposure to seasonal photoperiods or by salinity levels relevant to their estuarine environment (35 and 17ppt). Thus, I reject my hypothesis that salinity and/or photoperiod affects the diel cycle activity of mummichogs. The mummichog I studied appear to have a free-running activity pattern that is independent of the day/night cycle.

Although my study showed that there was no significant difference in activity between day and night, other studies have showed that mummichogs have shown a nocturnal pattern (Reeve and Speers-Roesch, Unpublished). In this study, the mummichogs were exposed to a winter photoperiod with a 35-salinity level while cooling the water by 1°C every day till the end of the experiment. Although my study looked at the activity level in winter photoperiod at 35-salinity level, an important difference between the two studies is the reduction in temperature. In my study, the mummichogs were acclimated to a consistent 14°C throughout the whole experiment. This could suggest that temperature influences the diel cycle patterns of mummichogs. Another important distinction is that the acclimation time in my study was longer. This extra time of acclimation might have let the mummichogs get back to more normal patterns of activity level of no difference between night and day.

Temperature has been known to be a critical environmental factor in the ecology of fish, where it is known to affect their activity level and their metabolic rates (Bartolini et al., 2015; Dadras et al., 2017). In a study where they examined the effect of temperature on activity of cunner, they found that their diel pattern was dampened with the decreasing temperature (Speers-Roesch et al., 2018). Fish are considered to have a plastic diel pattern where species or even individuals can have a variation of diel pattern (Reebs, 2002). Studies have shown the plasticity of diel pattern in salmonids, where they showed a more diurnal behavior during summer conditions and a decrease in daytime activity showing a more nocturnal pattern when exposed to winter conditions (Bremset, 2000; Godin, 1984). Reeve and Speers-Roesch (Unpublished) found that pumpkinseed sunfish showed a shift in spontaneous activity from a more diurnal patter towards a nocturnal one in response to acute cooling. Generally during warm temperatures, different species of fish such as pumpkinseed sunfish (*Lepomis gibbosus*) have shown a diurnal cycle (Collins and Hinch, 1993) while American eels (*Anguilla rostrata)* have a nocturnal cycle (Tomie et al., 2017). It appears that a decrease in daytime activity and an increase in nighttime activity is in response to cooling and other temperature changes in fish species, which may explain the nocturnal pattern seen by Reeve and Speers-Roesch (unpublished) relative to my free-running activity pattern.

Previous studies have suggested that mummichogs are a diurnal species where they show more activity during the day compared to the night. In a study where they measured the activity levels of mummichogs both individually and in groups, it was found that all the fish showed a higher activity level during the day (Kavaliers, 1980). A few studies have quantified mummichog diel patterns by examining at their feeding habits, where they found that mummichogs tend to have a fuller gut during the day compared to night, suggesting a diurnal cycle (Weisberg et al., 1981). Although the mummichogs in my study were tested at different salinity levels, other studies have suggested that their feedings habits could be driven by tides (Butner and Brattstrom, 2016). Also, other studies have suggested a diel cycle in mummichogs based on their abundance during day and night, where they found a higher abundance during the day (Hlapin, 1997). Due to estuarine environments being subjected to change due to varying environmental conditions, the diel pattern of mummichogs may be plastic but only under the influence of many interacting factors.

Nonetheless, Kavaliers' lab study showed a diurnal activity pattern in mummichogs, whereas in my lab study I found a free-running cycle. However, my study and Kavaliers (Kavaliers, 1980), and other previous studies, have all used different populations of mummichogs. Thus, perhaps the most logical conclusion is that diel activity patterns may vary among mummichog populations, possibly as a result of distinct environmental conditions that each population experiences. However, this needs to be researched further.

My study showed that mummichogs exposed to different levels of salinity and photoperiod showed no preference towards a specific diel cycle pattern, contradicting my hypothesis that salinity and/or photoperiod affects the diel cycle activity of mummichogs. My results were not in agreement with previous studies that observed the diel cycle patterns of mummichogs. Some studies have shown that mummichogs show a diurnal pattern while others show a nocturnal pattern. Previous studies have suggested that temperature could affect the diel cycle patterns of fish species. Future studies should consider the effect of temperature on the diel cycle pattern of mummichogs and carry out careful comparative re-assessments of the diel activity patterns of different mummichog populations that have been previously studied. Since mummichogs are one of the most important species in estuarine environments, knowing their daily patterns such as foraging and mating and how they are affected based on different environmental conditions could help us better understand the resilience of an estuarine food web, especially in the face of climate change.

References

Anderson, T. W. and Sabado, B. D. (1995). Correspondence between food availability and growth of a planktivorous temperate reef fish. *J. Exp. Mar. Bio. Ecol.* **189**, 65–76.

Bartolini, T., Butail, S. and Porfiri, M. (2015). Temperature influences sociality and activity of freshwater fish. *Environ. Biol. Fishes* **98**, 825–832.

Biswas, A. K. and Takeuchi, T. (2002). Effect of different photoperiod cycles on metabolic rate and energy loss of fed and unfed adult tilapia *Oreochromis niloticus*: Part II. *Fish. Sci.* **68**, 543–553.

Boeuf, G. and Le Bail, P. Y. (1999). Does light have an influence on fish growth? *Aquaculture* **177**, 129–152.

Bremset, G. (2000). Seasonal and diel changes in behaviour, microhabitat use and preferences by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Environ. Biol. Fishes* **59**, 163–179.

Burnett, K. G., Bain, L. J., Baldwin, W. S., Callard, G. V., Cohen, S., Di Giulio, R. T., Evans, D. H., Gómez-Chiarri, M., Hahn, M. E., Hoover, C. A., et al. (2007). Fundulus as the premier teleost model in environmental biology: Opportunities for new insights using genomics. *Comp. Biochem. Physiol. - Part D Genomics Proteomics* **2**, 257–286.

Butner, A. and Brattstrom, B. H. (2016). Local Movement in Menidia and Fundulus Author(s): Alfred Butner and Bayard H. Brattstrom Source: **1960**, 139–141.

Childs, A., Cowley, P. D., Næsje, T. F., Booth, A. J., Potts, W. M., Thorstad, E. B. and Økland, F. (2008). Do environmental factors influence the movement of estuarine fish ? A case study using acoustic telemetry. **78**,.

Clark, K. L., Ruiz, G. M. and Hines, A. H. (2003). Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *J. Exp. Mar. Bio. Ecol.* **287**, 37–55.

Collins, N. C. and Hinch, S. G. (1993). Diel and Seasonal Variation in Foraging Activities of Pumpkinseeds in an Ontario Pond. *Trans. Am. Fish. Soc.* **122**, 357–365.

Dadras, H., Dzyuba, B., Cosson, J., Golpour, A., Siddique, M. A. M. and Linhart, O. (2017). Effect of water temperature on the physiology of fish spermatozoon function: a brief review. *Aquac. Res.* **48**, 729–740.

El-Sayed, A. F. M. and Kawanna, M. (2004). Effects of photoperiod on the performance of farmed Nile tilapia *Oreochromis niloticus*: I. Growth, feed utilization efficiency and survival of fry and fingerlings. *Aquaculture* **231**, 393–402.

Godin, J. G. J. (1984). Temporal variations in daily patterns of swimming activity and vertical distribution in juvenile pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Zool.* **62**, 72–79.

Hlapin, P. (1997). Habitat use patterns of the Mummichog, Fundulus heteroclitus, in New England. I. Intramarsh variation. *Estuaries* **20**, 618–625.

Kavaliers, M. (1980). Social Groupings and Circadian Activity of the Killifish , *Fundulus heteroclitus* Author (s): Martin Kavaliers Published by : The University of Chicago Press in association with the Marine Biological Stable URL : https://www.jstor.org/stable/1540759. **158**, 69–76.

Levin, P. S. (1994). Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Environ. Biol. Fishes* **40**, 271–281.

Marshall, W. S., Tait, J. C. and Mercer, E. W. (2016). Salinity preference in the estuarine teleost fish mummichog (*fundulus heteroclitus)*: Halocline behavior. *Physiol. Biochem. Zool.* **89**, 225–232.

Ovidio, M., Baras, E., Goffaux, D., Giroux, F. and Philippart, J. C. (2002). Seasonal variations of activity pattern of brown trout (*Salmo trutta*) in a small stream, as determined by radio-telemetry. *Hydrobiologia* **470**, 195–202.

Reebs, S. G. (2002). Plasticity of diel and circadian activity rhythms in fishes. *Rev. Fish Biol. Fish.* **12**, 349–371.

Reeve,C and Speers-Roesch,B. In prep. Inactivity as the convergent mechanism underlying the metabolic phenotype in winder dormant fishes. Unpublished.

Reynolds, W. W. and Casterlin, M. E. (1982). Thermoregulatory behaviour, diel activity and the relationship of spontaneous locomotor activity to temperature in the sea raven, *Hemitripterus americanus* (Gmelin). *J. Fish Biol.* **20**, 1–4.

Sakabe, R. and Lyle, J. M. (2010a). The influence of tidal cycles and freshwater inflow on the distribution and movement of an estuarine resident fish Acanthopagrus butcheri. *J. Fish Biol.* **77**, 643–660.

Sakabe, R. and Lyle, J. M. (2010b). The influence of tidal cycles and freshwater inflow on the distribution and movement of an estuarine resident fish *Acanthopagrus butcheri*. 643–660.

Schartl, M. (2014). Beyond the zebrafish: Diverse fish species for modeling human disease. *DMM Dis. Model. Mech.* **7**, 181–192.

Schulte, P. M. (2007). Responses to environmental stressors in an estuarine fish: Interacting stressors and the impacts of local adaptation. *J. Therm. Biol.* **32**, 152–161.

Sikkel, P. (2014). Diel emergence patterns of ecologically important , fish-parasitic , gnathiid isopod larvae on Caribbean coral reefs Diel Emergence Patterns of Ecologically Important , Fish-Parasitic ,.

Speers-Roesch, B., Norin, T. and Driedzic, W. R. (2018). The benefit of being still: Energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. *Proc. R. Soc. B Biol. Sci.* **285**,.

Thompson, J. S. (2019). Salinity affects growth but not thermal preference of adult mummichogs *Fundulus heteroclitus* . *J. Fish Biol.* 1–9.

Tomie, J. P. N., Cairns, D. K., Hobbs, R. S., Desjardins, M., Fletcher, G. L. and Courtenay, S. C. (2017). American eel (*Anguilla rostrata*) substrate selection for daytime refuge and winter thermal sanctuary. *Mar. Freshw. Res.* **68**, 95–105.

Valdimarsson, S. K., Metcalfe, N. B., Thorpe, J. E. and Huntingford, F. A. (1997). Seasonal changes in sheltering: Effect of light and temperature on diel activity in juvenile salmon. *Anim. Behav.* **54**, 1405–1412.

Veras, G. C., David, L., Murgas, S., Rosa, P. V., Gilberto, M., Soares, M. and Leon, J. A. S. (2013). Revista Brasileira de Zootecnia Effect of photoperiod on locomotor activity , growth , feed efficiency and gonadal development of Nile tilapia 1. 844–849.

Weisberg, S. B., Whalen, R. and Lotrich, V. A. (1981). Tidal and diurnal influence on food consumption of a salt marsh killifish *Fundulus heteroclitus*. *Mar. Biol.* **61**, 243–246.

Yetsko, K. and Sancho, G. (2015). The effects of salinity on swimming performance of two estuarine fishes, *Fundulus heteroclitus* and *Fundulus majalis*. *J. Fish Biol.* **86**, 827–833.