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Diel Littoral-Pelagic Movements by Juvenile Bluegills in a Small Lake

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NOTE

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Abstract

Diel littoral–pelagic migrations by juvenile fish have been suggested as a mechanism that optimizes the trade-off between predation risk and foraging return in open-water habitats. However, previous study designs have not been able to conclusively demonstrate this behavior in the field. We applied a horizontally oriented hydroacoustic transducer, set at the open-water edge of littoral vegetation, to observe diel fish behavior during two summers in Ridge Lake, Illinois, where the fish community is dominated by Largemouth Bass *Micropterus salmoides* and Bluegills *Lepomis macrochirus*. Based on acoustically tracked targets, most juvenile fish moved away from vegetated habitat at night and towards vegetation during the day. A greater number of predator-sized fish were observed in the open water during the day than at night and weak acoustic targets, most likely zooplankton, were more abundant in the open-water habitat at night. Therefore, it is likely that the reduced predator abundance and/or activity combined with potentially greater food availability in the open-water habitat prompted an offshore migration at night that was reversed after sunrise. Diel horizontal migration patterns could affect the timing and location of interspecific interactions in systems where they occur and further research is needed to determine whether diel migrations alter ecosystem function.

Many fishes change habitats in response to changes in their environment (see reviews by Dill 1987; Mittelbach and Chesson 1987; Sih 1987, 1994; Lima and Dill 1990). These habitat selection patterns can alter food web dynamics (Power et al. 1985; Werner 1991) and may ultimately alter community composition through subsequent changes in competitive or predatory interactions. Changes in habitat selection are most often attributed to alterations in foraging return or predation risk (Dill 1987; Mittelbach and Chesson 1987; Sih 1987, 1994; Lima and Dill 1990). The trade-off between foraging return and predation risk often results in reduced growth (Mittelbach 1981; Gotceitas 1990a; Savino et al. 1992; Diehl and Eklov 1995) as organisms select habitats that minimize the mortality-rate : foraging-rate ratio (Gilliam and Fraser 1987) rather than maximizing foraging return. However, most evaluations of these relationships have been conducted at coarse time scales (i.e., growing season).

Short-term (i.e., diel) habitat shifts that alter important community-level interactions may also occur for some fishes (e.g., Gaudreau and Boisclair 2000; Pekcan-Hekim et al. 2005; Gliwicz et al. 2006; Rypel and Mitchell 2007). Diel habitat changes are also important to consider when designing sampling protocols for management or research, as abundance estimates of a species that exhibits diel habitat changes could be heavily influenced by the time when a sample is collected. Despite the importance of measuring diel habitat use by fish, it is a difficult variable to measure accurately. Different habitats often require different gears for sampling (Hayes et al. 2012; Hubert et al. 2012). For example, seines or electrofishing are commonly used

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in littoral habitats, but are not effective in pelagic habitats where gill nets are more commonly used (Bonar et al. 2009). Sampling different habitats with different gears could allow diel changes in gear-specific sampling efficiency (Hayes et al. 2012; Hubert et al. 2012) to produce apparent changes in abundance when no such change actually existed. Even in cases where the same gear can be used in multiple habitats, habitat-specific biases in diel gear efficiency could still confound abundance estimates. Therefore, care must be taken when assessing diel habitat use that gear biases do not confound results.

Bluegill *Lepomis macrochirus* is an ecologically and economically important fish species that is often locally abundant. Largemouth Bass *Micropterus salmoides* is a common predator of Bluegill, and predation risk from this species often causes Bluegills to select densely vegetated habitats during daytime (Mittelbach 1981; Werner et al. 1983; Gotceitas and Colgan 1987). More recently, laboratory studies found juvenile Bluegills may alter their habitat use on a diel basis (Shoup et al. 2003). In this study, the amount of time spent in vegetated or open-water habitat varied with the rate of foraging return and predation risk, but in general, Bluegills spent more time in open water at night than they did during the day in the laboratory under all treatment conditions. Shoup et al. (2003) suggested these behaviors lead to diel onshore–offshore migrations by Bluegills in lakes; however, these habitat use patterns have not been definitively assessed in field studies. Only one study has sampled Bluegills in littoral and pelagic habitats during daytime and nighttime (Baumann and Kitchell 1974), using different gears in each habitat. Those investigators found the opposite pattern of Shoup et al. (2003). Therefore, the purpose of the current study was to further investigate diel habitat use by Bluegills in the field to see whether the habitat selection patterns observed in the laboratory (Shoup et al. 2003) occur in natural systems.

METHODS

Ridge Lake, Coles County, Illinois, is a 5.6-ha reservoir with a mean depth of 2.8 m and a maximum depth of 6.5 m. The lake typically exhibits thermal stratification from May to August with a thermocline at 2–3 m depth and a hypoxic hypolimnion. There is abundant vegetation in a well-defined littoral zone that extends 4–10 m from shore where the lake depth abruptly increases, forming distinct deep-water vegetation edges around much of the lake. Littoral vegetation is predominantly curly leaf pond weed *Potamogeton crispus* and coontail *Ceratophylum dimersum*, with lesser amounts of southern najas *Najas guadalupensis* and *Chara* spp. The fish community is primarily composed of Bluegill and Largemouth Bass, with lower abundances of adult Channel Catfish *Ictalurus punctatus* (no reproduction of Channel Catfish has ever been detected; all catfish are stocked at 200 mm TL and would be too large to be mistaken in the hydroacoustic signal for a juvenile Bluegill). Seine data from the fall of 2003 and 2004 ($N = 15$ seine hauls; 831 fish collected) indicated that 97% of the juvenile fish community was composed of Bluegills and electrofishing data from those same years ($N = 22$ samples; 238 fish $>$ 250 mm TL) indicated 98% of fish $>$ 250 mm TL were Largemouth Bass (D. H. Wahl, unpublished data). No other fish species were found in Ridge Lake.

Fish movements were assessed using a Biosonics DT hydroacoustic system with a 208-kHz single-beam transducer (6.3° beam angle). Samples were taken approximately 2–3 d per week from July through August in 2003 and June through August in 2004 after littoral vegetation was established and before it senesced in the fall. The transducer was deployed horizontally (at approximately a 30° angle below surface to avoid surface interference) at the deep-water edge of the vegetation (i.e., transducer was surrounded by vegetation but had no macrophyte stems in front of it). The transducer was oriented towards open water approximately 0.5 m below the surface by attaching it to a T-post embedded in the sediment. The acoustic beam was roughly parallel to the surface and just deep enough to avoid interference from waves, and sampled from the pelagic–littoral ecotone to a depth of 10 m into the pelagic habitat (about 10–15% of the distance across the pelagic zone in this part of the lake). Data from the echosounder were recorded on a laptop computer housed in a boat tied to an onshore tree approximately 4 m from the stationary transducer (far enough that it would not influence fish behavior). Hydroacoustic data were collected at 2 pulses/s, with a 0.4-ms pulse width, −63 dB sensitivity threshold, and a 40 log R time-varied gain. Acoustic data were collected for 24–72 h (depending on weather and battery life) on 15 separate occasions over the two summers (total of 576 h sampled).

Juvenile fish targets were validated using seining, electrofishing, and purse-seine samples. Bluegills made up 100% of the juvenile fish (<90 mm) sampled in open-water habitat. Therefore, we made a simplifying assumption that all juvenile fish targets observed in the acoustic data were Bluegills. Although it was possible a few of the observed fish were juvenile Largemouth Bass (the only species in the lake for which juveniles were ever detected), this would not be expected to occur often enough to bias the results of the study.

Raw acoustic intensity data were processed using Echoview 5 (Myriax Pty.) to identify targets, estimate target-strength distributions, and determine the distance and direction targets moved while in the sound beam (closer to or farther from the transducer). Within Echoview, absorption coefficients were applied to compensate for temperature effects on sound speed. At nighttime, vertically migrating zooplankton were readily identifiable as resonant scatters during this period. Therefore, a background subtraction filter, as described in Boswell et al. (2008), was applied prior to target detection. Although Boswell et al. (2008) applied the filtering process to the volume backscattering strength data (20 log R), we applied the same filtering technique to the 40 log R data, which resulted in a target strength echogram with ambient background levels removed, facilitating single target detection and tracking on targets that exceeded background noise (i.e., following a single target through time and space). An alpha–beta tracking algorithm was applied to the single targets that satisfied the tracking criteria in Table 1. Fish tracks

TABLE 1. Single target tracking parameters used in analyses of Bluegill movements.

Parameter	Value
Target strength	−63 dB
Single target detector:	
Pulse length determination level	6 dB
Minimum normalized pulse length	0.6
Maximum normalized pulse length	1.7
Maximum beam compensation	12 dB

were then manually verified and exported into text files for further analysis of target strength (i.e., acoustic representation of fish length) and direction of movement (i.e., toward or away from the littoral zone).

To relate horizontal target strengths with fish size, individual Bluegills and Largemouth Bass of known size were tethered on monofilament fishing line 4.5–9.0 m in front of the transducer in Ridge Lake to generate target-strength distributions for juvenile Bluegills (<90 mm TL) and adult Largemouth Bass (>250 mm TL). Additional target strengths for juvenile fish with different aspects facing the transducer were measured in large tanks (approximately 1.5 m from the transducer). From these data, we established that juvenile fish had mean target strengths between −57 and −52 dB, and Largemouth Bass > 250 mm had mean target strengths ≥ −48 dB, providing clear separation between these groups of targets (a 3-dB change is a doubling of sound intensity, so our 4-dB separation is quite distinct). These measurements are consistent with estimates of mean horizontal target strengths from other studies (Love 1969; Frouzova et al. 2005; Boswell and Wilson 2008). Further refinement of Bluegill size-classes was not possible as it would have resulted in overlapping target strengths among size-groups.

We expected fish behavior to more closely relate to sunrise and sunset than time of day. Therefore, we recoded time of day into 10 intervals that related to the time of sunrise and sunset. Daylight hours were divided into six equal intervals and nighttime hours were divided into four equal intervals. This produced 10 intervals/d that ranged from 2 h 13 min to 2 h 39 min in duration where interval 1 always began at sunrise and interval 7 always began at sunset. The number of intervals selected traded off the precision of temporal information against the number of targets detected per interval. Using 10 intervals gave a resolution of approximately 2.5 h while still providing an average of 23 fish in each interval on each sampling date.

Within each time interval, the number of juvenile-sized tracks (sequential target returns) from targets that moved at least 0.1 m closer to or farther from the transducer were counted on each sample date ($N = 15$ dates). Target tracks were used instead of counts of fish located at different distances from the transducer to avoid detection bias related to the sound cone shape (smaller area near transducer than far from transducer) and because nighttime samples may have missed some small targets located far from the transducer due to resonance from zooplankton (which was not a problem during daytime samples). By confining the analysis only to those fish that were detected, detection bias could not confound diel patterns. No significant differences in movement patterns were observed based on distance of fish from the transducer ($F_{4, 127} = 1.37$, $P = 0.25$) or on fish sizes (target strength; $F_{4, 127} = 0.50$, $P = 0.74$), indicating no bias should result from resonance that masked some small fish at the far end of the acoustic beam. From these counts of fish moving in each direction, a single response variable, the proportion of fish moving away from the transducer, was calculated (values were square transformed [$X' = X^2$] to adjust for proportionality between standard deviations and means). We then performed a time-series analysis using trigonometric regression (Cox 2006) to test for diel patterns in the proportion of Bluegills moving offshore. Trigonometric regression uses linearized combinations of sine and cosine terms to conduct a Fourier analysis via generalized linear modeling. We used SAS Proc Mixed (Dickey 2008; SAS 2011) with repeated measures to account for date effects (i.e., 10 time intervals were specified as repeated measurements on dates). Several trigonometric models were tested starting with a model that only included the fundamental frequency (1/10; one cycle per day [10 time intervals]) and successively adding harmonic frequencies up to the Nyquist frequency (5/10; one cycle per two time intervals, the largest frequency that would be meaningful given the resolution of the time measurements). Only models with significant slopes ($P \leq 0.05$) were considered. If more than one model was significant, the most parsimonious model was selected using the Akaike information criterion (AIC). To measure the proportion of variance explained by the model, we calculated a pseudo-R^2 from residual estimates of the full model and a null model with only an intercept parameter (Singer and Willett 2003). The number of predator-sized targets (square transformed) were also counted within each time interval and tested with trigonometric regression. We used predator counts rather than percent movement as predator data were collected to assess open-water predator abundance and/or activity (a surrogate for predation risk) rather than movement patterns.

RESULTS

A total of 41,019 fish tracks were recorded from 15 different sampling events. Movement of juvenile Bluegills between littoral and pelagic habitat was best described by a sinusoidal model with only the fundamental frequency (1/10; one complete cycle per day; Figure 1). This model explained 83.4% of the variability in Bluegill movements. All other models (i.e., those including harmonic frequencies) had insignificant slopes. The majority of juvenile Bluegills observed were moving offshore during all nighttime intervals (intervals 7–10). The majority of observed fish were moving towards the littoral zone during daytime intervals (intervals 2–5). Time intervals around dawn (interval 1) and dusk (interval 6) had a similar proportion of individuals moving in both directions.

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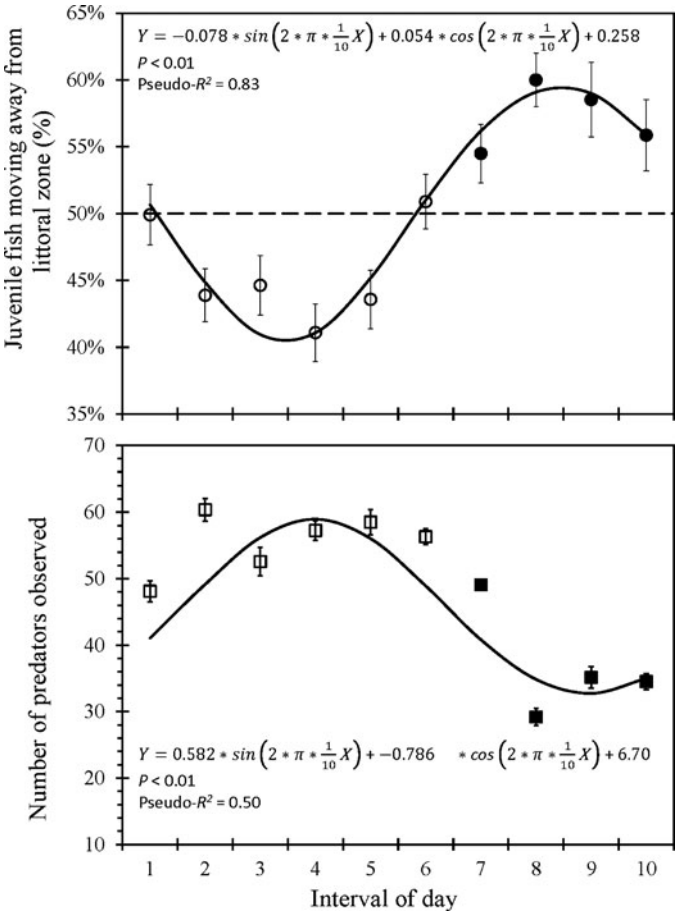

FIGURE 1. Diel pelagic predator abundance and/or activity and juvenile fish movement behavior measured by horizontal hydroacoustics in Ridge Lake, Illinois. The top panel is the mean proportion of juvenile fish moving away from the littoral zone. The horizontal dashed line indicates where equal numbers of individuals were observed moving towards and away from the littoral zone. Data below this line indicate the majority of individuals were moving towards the littoral zone; data above this line indicate the majority were moving away from the littoral zone. The bottom panel is the mean number of predators observed in open water (to quantify open-water predation risk, movement of predators was not considered). Daylight hours were divided into six equal intervals (white symbols) and nighttime hours were divided into four equal intervals (dark symbols) to produce 10 intervals (ranging from 2 h 13min to 2 h 39 min); interval 1 always began at sunrise and interval 7 always began at sunset. Error bars indicate $\pm$ 1 SE.

The number of predators observed in the offshore habitat (a function of predator abundance and activity) was used as an index of potential predation risk to Bluegills. The number of predators was also best described by a sinusoidal model with only the fundamental frequency (1/10; one complete cycle per day), which explained 50% of the variability in offshore predator abundance (Figure 1). All other models had insignificant slopes. Offshore predator counts had approximately the inverse of the pattern observed for the offshore movement of Bluegills (Figure 1). Peak predator counts in open water were observed during midday hours and the lowest values occurred during mid- to late nighttime.

DISCUSSION

Previous laboratory studies found Bluegills spent more time in open water at night and more time in simulated vegetation during the day even though food was only available in the open water habitat (Shoup et al. 2003). Bluegills in the laboratory are more likely to venture into high-risk, high-foraging return open-water habitats at night. This behavior could lead to diel onshore–offshore migrations (Shoup et al. 2003). Our field study was consistent with this prediction as we found that the majority of juvenile Bluegills moved in an offshore direction at night and closer to littoral habitat during the day.

Although our study was not designed to directly test the mechanisms involved, it is possible that changes in foraging return and/or predation risk were cues that were at least in part responsible for this behavior, as predicted by Shoup et al. (2003). When large-bodied zooplankton are abundant in the pelagic zone (Mittelbach 1981; Werner and Hall 1988), or when littoral habitat has complex cover (Gotceitas 1990b; Pothoven et al. 1999; Shoup et al. 2007, 2012), Bluegills typically experience greater returns by foraging in the pelagic zone, but are often confined to vegetation during daylight hours by predation risk (Mittelbach 1981; Werner et al. 1983; Gotceitas and Colgan 1987). We observed nocturnal acoustic returns consistent with large vertically migrating (Lampert 1989; Dodson 1990) zooplankton species (i.e., -64 – -60 dB; Echmann 1998; Jones and Xie 1994; Knudsen et al. 2006), and sampling zooplankton on two dates ($N = 4$ for each time of day) validated these targets as primarily *Chaoborus* and calanoid copepods (D. E. Shoup, unpublished data). Additionally, open-water predation risk may have been reduced at night because Largemouth Bass (the dominant predator in our system) are less efficient at capturing Bluegills at nighttime light levels (Howick and O'Brien 1983; McMahon and Holanov 1995), and we observed a reduction in the number of predator-sized targets in our hydroacoustic data during nighttime (either a result of lower abundance or reduced activity by predators at night). Further research is warranted to determine whether these observed diel changes in acoustic data for zooplankton- and predator-sized targets constitute diel changes in pelagic foraging return and/or predation risk for Bluegills that might explain the mechanism leading to the habitat use patterns we found.

Other studies have also suggested that Bluegills exhibit diel habitat shifts between littoral and pelagic habitats (Baumann and Kitchell 1974; Werner et al. 1977; Helfman 1981). However, these studies found Bluegills used littoral habitat at night and pelagic habitat during the day, the reverse of what we found and what was predicted by Shoup et al. (2003). One possible interpretation of these conflicting results is that they are a result of the different gears used among studies. Two of these three studies (Werner et al. 1977; Helfman 1981) used divers to observe Bluegill habitat use. Bluegills may have allowed divers to approach closer when they were near protective cover (vegetation), thus increasing detectability for this habitat. At low light levels (i.e., dawn and dusk), the increased detectability

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of Bluegills near vegetated habitat could give the appearance that more fish were located in this habitat. These observational studies also did not include data from nighttime as light levels were too low for human observation. We observed the greatest proportion of offshore movement during the middle of the night when these studies could not make observations. A third study that found the inverse of our results (Baumann and Kitchell 1974) used different gear types to sample the two habitats. Electrofishing was used in littoral habitat, and a benthic trawl was used in pelagic habitat. Bias between these two gears could have produced these apparent results. Electrofishing catch rates during nighttime are typically higher for most species, including Bluegill (Burkhardt and Gutreuter 1995; Dumont and Dennis 1997), presumably due to reduced gear avoidance at night. Similarly, nighttime benthic trawls may underestimate the abundance of pelagic fish if they occupy the water column above the depth of the trawl. Bluegills would likely be in the upper half of the water column at night to encounter the light levels needed for foraging (Vinyard and O'Brien 1976).

Although the different diel habitat-use patterns observed by previous studies could have resulted from gear bias, it is also possible that diel habitat use by Bluegills varies across systems. Habitat-specific conditions, such as foraging return or predation risk, could vary among systems in a way that may alter Bluegill behavior. Baumann and Kitchell (1974) suggested that offshore zooplankton abundance was higher in their system during the day (although this was not directly measured), which is opposite of the zooplankton pattern we observed in our hydroacoustic data. Some lakes also do not have vertical zooplankton migrations (Dodson 1990) and may therefore have no diel change in pelagic foraging return. There may also be lake-to-lake variation in the diel pattern of offshore predation risk. Our study system was also smaller (6.5 ha) than the lake studied by Baumann and Kitchell (1974; Lake Wingra, 137 ha) or Helfman (1981; Cazenova Lake, 475 ha); lake size could be associated with a variety of habitat differences that might influence migration patterns. Studies in additional lakes are warranted to determine the pervasiveness of diel littoral–pelagic migrations by Bluegills.

Diel habitat changes by fish species, such as those we documented for Bluegill, are important to understand as they could produce unexpected ecological effects and should be considered when designing sampling protocols. For example, the effects of diel horizontal migrations could alter food web dynamics by producing spatially subsidized food webs (Polis et al. 1997) that allow the production of more fish in migrating populations than would be possible using the food resources of any one habitat. Alternatively, by foraging in multiple habitats, migrating species may have a wider range of competitive interactions than has previously been recognized, potentially leading to erroneous management decisions when migrations are not considered. Diel habitat changes by Bluegills could also lead to a net nutrient flux between littoral and pelagic habitats when they forage in one habitat and excrete nutrients during the digestive process in another habitat (Shoup 2001). Although these potential ecological effects are beyond the scope of the current study, our results suggest future research is needed to better understand these ecosystem processes in light of the diel migration behaviors we have documented. Further, our results suggest that diel periodicity should be considered when sampling for research and management purposes. For example, diet studies used to assess the availability of food or potential for competitive interactions are often conducted with daytime fish samples, and our study highlights the importance of sampling during both daytime and nighttime.

We found that juvenile Bluegills conduct horizontal diel migrations between littoral and pelagic habitats that negatively correlate with the number of piscivore-sized targets observed in the pelagic habitat. Manipulations to enhance sport fish populations could significantly alter predation risk in littoral or pelagic habitats, which could in turn alter diel habitat use by juvenile fishes. Juvenile fish migrations could ultimately change food web linkages, competitive interactions, and/or nutrient dynamics in lakes. The potential for these types of interactions support the current movement towards ecosystem-based management in marine systems (Francis et al. 2007; Curtin and Prellezo 2010) and its application to inland fisheries (Beard et al. 2011).

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