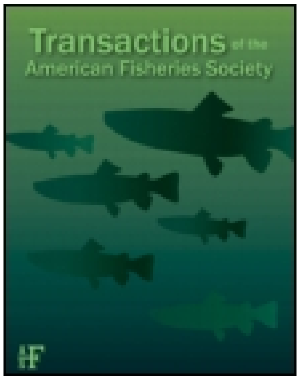

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Characterizing Seasonal Habitat Use and Diel Vertical Activity of Lake Whitefish in Clear Lake, Maine, as Determined with Acoustic Telemetry

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ARTICLE

Characterizing Seasonal Habitat Use and Diel Vertical Activity of Lake Whitefish in Clear Lake, Maine, as Determined with Acoustic Telemetry

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Abstract
Seasonal and daily vertical activity of lake whitefish *Coregonus clupeaformis* was studied in Clear Lake, Maine (253 ha), using acoustic telemetry from November 2004 to June 2009. Twenty adult lake whitefish were tagged with acoustic tags that had either a depth sensor or both depth and temperature sensors to assess vertical habitat use at a seasonal and daily resolution. Vertical habitat selection varied seasonally and was strongly influenced by temperature. Between December and April, when the lake was covered with ice, surface temperature was below 2°C and tagged individuals occupied deep areas of the lake (∼15 m). After ice-out, fish ascended into shallow waters (∼5 m), responding to increased water temperature and possibly to greater foraging opportunity. When surface water temperatures exceeded 20°C, fish descended below the developing thermocline (∼9 m), where they remained until surface temperatures fell below 20°C; fish then ascended into shallower depths, presumably for feeding and spawning. Through the winter, fish remained in thermal habitats that were warmer than the surface temperatures; in the summer, they selected depths with thermal habitats below 15°C. Though the amplitude varied greatly across seasons, lake whitefish displayed a strong diurnal pattern of activity as measured by vertical velocities. Fish were twofold more active during spring, summer, and fall than during winter. Lake whitefish exhibited diel vertical migrations, rising in the water column during nighttime and occupying deeper waters during the day. This pattern was more pronounced in the spring and fall and far less prominent during winter and summer. The strong linkage between temperature and habitat use may limit the current range of lake whitefish and may be directly impacted by climatic change.

Conservation and management of fish species and ecosystems depend on an understanding of habitat use and fish distribution in relation to the environment. Lake whitefish *Coregonus clupeaformis* (Salmonidae) are distributed across the North American continent from the northeastern United States through Canada (Evans at al. 1988; Edsall 1999a, 1999b). Populations of lake whitefish in Maine, USA, are considered to be located along the southern extreme of the species' continental range and are restricted to the north-central part of the state, occurring in headwater lakes of two major river systems. Many lakes in Maine once had strong lake whitefish populations, but over the past few decades,

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creel surveys and inventory data have indicated marked declines.

Lake whitefish typically reach ages of 10 years or more and attain sexual maturity between 3 and 6 years of age. Sexually mature adults spawn in shallow shoals or tributaries between late October and November when water temperatures are below 6°C (Nester and Poe 1984; Anras et al. 1999). Spawning is thought to take place at night over a period of about a week (Hart 1931); however, more recent data suggest that spawning is independent of time or daylight cycles (Anras et al. 1999). As a species, lake whitefish are not very tolerant of warmer water temperatures. Lake whitefish critical swimming speed and oxygen consumption are maximized at 12°C (Bernatchez and Dodson 1985). Studies of larval lake whitefish indicate that the highest larval survival occurs at 10°C and the highest growth occurs at 18°C (Edsall 1999a); juvenile lake whitefish actively selected temperatures between 15.6°C and 16.8°C (Edsall 1999b). Based on data compiled from three sources, Christie and Regier (1988) suggested that the fundamental thermal niche for lake whitefish is between 10°C and 14°C.

Habitat use by fish at both daily and seasonal scales can be related to spawning, feeding, and growth (Casselman et al. 1981; Hofmann and Fischer 2002). Critical to fulfilling their life history requirements, many coldwater fish species shift seasonally between nearshore and offshore habitats while also moving between shallow and deep waters for feeding and spawning (e.g., Anras et al. 1999; Hofmann and Fischer 2002). Along with seasonal shifts, ontogenetic habitat shifts may occur between shallow littoral zones and deeper benthic or pelagic zones (Sandlund et al. 1992, 1995).

Fish distribution and associated habitat shifts may be further influenced by abiotic factors (Næsje et al. 1991). For many species, temperature is the primary exogenous driver of fish distribution (Scherer and Harrison 1988; Baldwin et al. 2002; Nowak and Quinn 2002). Fish selectively occupy distinct thermal habitats within lakes and use behavioral thermoregulation in order to occupy thermal habitats that favor biological processes (Neill 1979). These preferred habitats have been termed the "fundamental thermal niche″ (Magnuson et al. 1979). Measures of fundamental thermal niche are often predicted using final preferendum temperatures and the optimum temperature for growth; these are determined by laboratory studies in which feeding and temperature can be artificially controlled (Magnuson et al. 1979; Christie and Regier 1988). The fundamental thermal niche can therefore be thought of as a range of temperatures in which fish activity and metabolism are maximized. In stratified lakes, water temperature varies vertically with depth. Consequently, vertical habitat use is not only influenced by but may be constrained to depths with temperatures that are within the fundamental thermal niche of the species.

At seasonal and daily temporal scales, the effect of climate change on habitat conditions presents a major threat to coldwater fish populations (Graham and Harrod 2009). Predictive models of climate change suggest an increase in air temperature between 3.5°C and 4.2°C in the next 30–50 years, which will cause major thermal changes to aquatic environments (Boer et al. 1992). Climatic changes will delay the onset of ice formation, shorten the duration of ice coverage, and advance the date of ice-out (De Stasio et al. 1996). Likewise, these changes will increase peak summer temperatures and the duration and strength of thermal stratification. Models for small, north-temperate lakes have shown that increases of 2–9°C can result in major habitat changes (De Stasio et al. 1996; Jansen and Hesslein 2004). Jansen and Hesslein (2004) hypothesized that increasing air temperatures could (1) reduce the number of spring days before surface water temperatures pass a critical temperature threshold and (2) maintain higher summer temperatures for longer periods of time. This extended duration of high temperatures may result in greater lake productivity but at the cost of dissolved oxygen problems in the hypolimnion, thus degrading habitat for coldwater fish species that are limited to depths below the thermocline (De Stasio et al. 1996).

In addition, biotic factors such as food availability, competition, and predation further affect habitat use (Hayes et al. 1996; Jackson et al. 2001). Habitat selection by fish is often based on opportunity for growth and high survival, as are provided by habitats that have abundant prey with few competitors (Crowder and Magnuson 1982; Sydänoja et al. 1995; Warner and Quinn 1995). Additionally, fish select habitats that allow for predator avoidance (Werner et al. 1983; Jackson et al. 2001). The interaction of abiotic and biotic factors affects fish habitat selection and ultimately determines the realized niche for the species.

On a finer temporal scale, diel patterns of habitat use and activity are primarily driven by prey availability and light intensity (Gjelland et al. 2004; Ohlberger et al. 2008). Planktivorous fish actively move between deep habitats, which are occupied during the daytime to reduce predation, and shallow habitats, which are occupied during the night to increase foraging opportunities. Piscivorous fish have been shown to follow similar diel vertical migrations that optimize growth and foraging by tracking the movements of planktivorous prey (Jensen et al. 2006).

The well-defined thermal niche of lake whitefish is likely to be strongly associated with behavioral patterns at both seasonal and daily scales. The availability of essential habitats and environmental conditions that are appropriate for lake whitefish growth, survival, and reproduction is critical for continuation of individual populations. Based on our understanding of lake whitefish temperature preferences, we hypothesized that temperature will have a strong influence on vertical habitat selection by adult lake whitefish. We further hypothesized that diel changes in activity rates and habitat use are associated with lake whitefish feeding and life history behaviors. Our work presents 6 years of telemetry data showing seasonal and diel habitat use and behaviors of lake whitefish in a small lake system. This long-term study fills a gap in the understanding of how lake whitefish populations use the various vertical habitats available within lakes.

METHODS

Study system.—Clear Lake is a small lake system (253 ha) located in unorganized township T10 R11 WELS in Piscataquis County, Maine (46°31′16.02″N, 69°7′33.97″W). Clear Lake is a low-color (9 standard platinum units), oligotrophic lake (total phosphorus = 4 μg/L) with a mean depth of 8.8 m and a maximum depth of 26.2 m (PEARL 2011). Three years of water quality data (1989, 1996, and 1999) taken in mid-August show that a thermocline consistently begins at depths of 7–8 m. The fish community in Clear Lake consists of two top predators: the lake trout *Salvelinus namaycush* and brook trout *Salvelinus fontinalis*. Additionally, there is a benthic fish community consisting of lake whitefish, brown bullheads *Ameiurus nebulosus*, burbot *Lota lota*, slimy sculpin *Cottus cognatus*, and white suckers *Catostomus commersonii*. The prey fish community includes eastern blacknose dace *Rhinichthys atratulus*, northern redbelly dace *Phoxinus eos*, creek chub *Semotilus atromaculatus*, lake chub *Couesius plumbeus*, rainbow smelt *Osmerus mordax*, and threespine sticklebacks *Gasterosteus aculeatus*.

We divided the study timeline into four periods (I–IV) during which we observed distinct fish behavior and habitat use. The four periods each have environmental characteristics associated with each of the four seasons but do not follow strict calendar solstice and equinox dates. These periods were determined subjectively based on environmental conditions and periods of stratification and mixing in Clear Lake. Period I (overwinter; December–April) was characterized by ice cover and cold surface water temperatures. Period II (spring transition; May–June) was marked by a loss of ice cover and rising water temperatures. During period III (summer; July–September), the lake was characterized by peak water temperatures and a long photoperiod. Finally, period IV (fall turnover; October–November) was again a transitional period in which temperatures and photoperiod decreased.

Fish capture and telemetry.—Lake whitefish were collected during spawning runs from 2004 to 2006 using 1.5-m-deep trap nets with a 30.5-m lead net. Trap nets were set in 1–2 m of water along known spawning migration corridors. Trap nets were routinely checked once or twice per week starting on October 15 and ending when ice restricted access to the nets (typically the third week of November). Fish were removed from the trap nets and transported to shore for processing. Lake whitefish were anesthetized using a buffered solution of tricaine methanesulfonate (MS-222; 100 mg/L; 0.20-mM $NaCO_3$, pH = 7.0). Fish fork length was measured to the nearest millimeter, and scales for age determination were removed above the lateral line and just posterior to the dorsal fin. Scales of tagged fish were pressed in acetate with a heated hydraulic press. Ages of tagged fish were estimated by identifying annuli on the scale impressions using Jearld's (1983) criteria. Aging was performed by two independent readers; when disagreement occurred, a third reader analyzed the scales to facilitate a consensus.

To tag the lake whitefish, a small (<2 cm), ventral incision was made posterior to the pectoral girdle by using a sterile scalpel. The acoustic tag was manually inserted through the incision. The area of incision was swabbed with providine solution before and after surgery. Two sutures of coated Vicryl 4–0 absorbable sutures (Ethicon, Inc., Somerville, New Jersey) were used to close the incision; fish were then allowed to recover in aerated source water for 10–15 min. The surgery was typically performed in less than 2 min, and no immediate mortalities were observed. Once they recovered, the fish were released approximately 1 km from the point of initial capture so as to avoid immediate recapture.

Each fish was tagged with either a Vemco V9P tag (Vemco, Halifax, Nova Scotia; 2004: n = 10; 2005: n = 2; 2006: n = 6) or a Vemco V9TP tag (2006: n = 2), allowing for unique identification of tagged fish (Table 1). The V9P tags transmitted fish identification and fish depth information to receivers at a distance of up to 500 m. The V9TP tags similarly transmitted identification and depth data, but they additionally transmitted the water temperature at that depth. In the first year of the study, the acoustic transmitters were programmed with a random ping rate between 40 and 120 s. The tags had a theoretical maximum detection rate of 1,080 detections/d, which not only shortened tag life (365 d) but also filled the memory of some receivers in less than 6 months. During subsequent years, tags were programmed with a random ping rate between 150 and 300 s, which resulted in a longer duration of tag life (930 d) and receiver capacity. The V9 tags with longer ping rates had a lower theoretical maximum detection rate of 384 detections/d. In 2006, four additional tags were used that had a faster ping rate of 40–80 s, resulting in a maximum detection rate of 1,440 detections/d.

Five Vemco VR2 receiver units were deployed in Clear Lake beginning in November 2004 for year-round passive detection (Figure 1). Data were collected from November 2004 to June 2009. For a period of 9 weeks between June and August 2005, three receivers were nonfunctional due to expended memory capacity. Data from receivers were downloaded annually and imported into a Microsoft Access database.

Rules for exclusion of incomplete or false data were based on biologically meaningful criteria. The first rule for data exclusion was that data from dead fish were removed. Visual interpretation of the raw data identified the time at which an individual fish ceased vertical movements; data from that point on were omitted. Fish that displayed irregular behaviors leading to suspicions of imminent mortality were also excluded. Data associated with those fish were excluded from analysis and are not presented here. For the second rule, data suggesting that the fish occupied impossible depths were excluded. Depth data were from an older, unverifiable source, so all recorded depths of 30 m or greater were removed, since Clear Lake is believed to have a maximum depth of only 26 m (PEARL 2011). Finally, further data exclusion was performed for each of the analyses based on

TABLE 1. Sex, age, and fork length (FL) of lake whitefish tagged in Clear Lake, Maine, during each year. Maximum theoretical detection rate is based on the average ping rate (s) over the course of a day. The observation period is the number of days from which observation data were used for analysis; the mean number of detections per day (with interquartile range) across all years of data is shown. Percentage of theoretical detection rate indicates the relationship between the theoretical maximum detection and actual detection rates.

							Actual detections per day		
Year	Sex	Age (years)	FL (mm)	Tag type[b]	Maximum theoretical detection rate (detections/d)	Observation period (d)	Median	Interquartile range	Percentage of theoretical detection rate
2004	M	7+	363	V9P-2L	1,080	274	153	19–502	14
	F	6+	380	V9P-2L	1,080	191	97	25–336	9
		7+	365	V9P-2L	1,080	191	314	134–597	29
		7+	378	V9P-2L	1,080	340	162	17–439	15
		7+	379	V9P-2L	1,080	222	528	134–740	49
		7+	385	V9P-2L	1,080	582	38	1–198	4
		7+	387	V9P-2L	1,080	221	415	6–700	38
		8+	390	V9P-2L	1,080	385	185	41–648	17
		8+	395	V9P-2L	1,080	433	319	117–488	30
		12+	414	V9P-2L	1,080	640	324	159–526	30
2005	M	7+	395	V9P-2L	384	234	144	33–228	37
		8+	388	V9P-2L	384	903	47	13–109	12
2006	M	3+	283	V9P-2L	1,440	733	172	21–458	12
		3+	302	V9P-2L	1,440	185	539	51–881	37
		4+	301	V9P-2L	1,440	196	227	126–510	16
		4+[a]	301	V9TP-2L	384	657	106	35–209	28
		4+	307	V9P-2L	1,440	787	193	29–426	13
		8+	383	V9P-2L	384	173	299	271–325	78
		9+	395	V9P-2L	384	946	73	0–195	19
		9+	415	V9TP-2L	384	510	57	1–137	15

[a] Temperature data for this individual are represented in Figure 2C.
[b] The Vemco V9P tags transmitted depth data; V9TP tags transmitted depth and temperature data.

the number of detections within a reasonable time period for biologically meaningful statistics as described below.

Seasonal depth data analysis.—Detection data for individuals were assessed for seasonal depth distribution throughout the year. Data for each fish were grouped by standard week based on the Julian date system, with week 1 beginning on January 1 and ending on January 7. Detection data for each day on which an individual fish had fewer than 15 detection events were excluded from the analysis. The 15-detection threshold was used to identify a minimum number of location events that would describe an individual fish's habitat selection. The distribution of depth data deviated from normality, so medians were used to assess the measure of central tendency for the population and in analyses (Shapiro–Wilk test statistic = 0.53, n = 1,916, $P < 0.000$). The 25th and 75th percentiles of weekly depths of tagged fish were calculated using the median weekly depths. Fish median depth data were analyzed for differences among periods using the nonparametric Kruskal–Wallis analysis of variance (ANOVA). Pairwise comparisons between individual periods were performed using the Mann–Whitney U-test. An α level of 0.05 was used for analyses.

During each year of the study (2004–2009), subsurface temperature was recorded at hourly intervals using a HOBO temperature logger (Onset Computer Corp., Bourne, Massachusetts) located on a dock mooring at the eastern shore of Clear Lake (Figure 1). Data loggers were located less than 1 m below the surface. Mean daily temperature was used to calculate the mean weekly temperature and SD.

Diel vertical migration analysis.—Each detection event was assigned a date with an associated night–day designation. For sunrise and sunset times, we used U.S. Navy data for Ashland, Maine (46°38′N, 68°23′W; USNO 2011). For the purpose of analysis, each date began at sunrise and continued to the next sunrise so that every date contained the full period of day and night. To accommodate changing photoperiods, detection events were standardized by the length of each day and night period. Standardization to "decimal time" was accomplished by (1) taking the difference between the time of the detection event

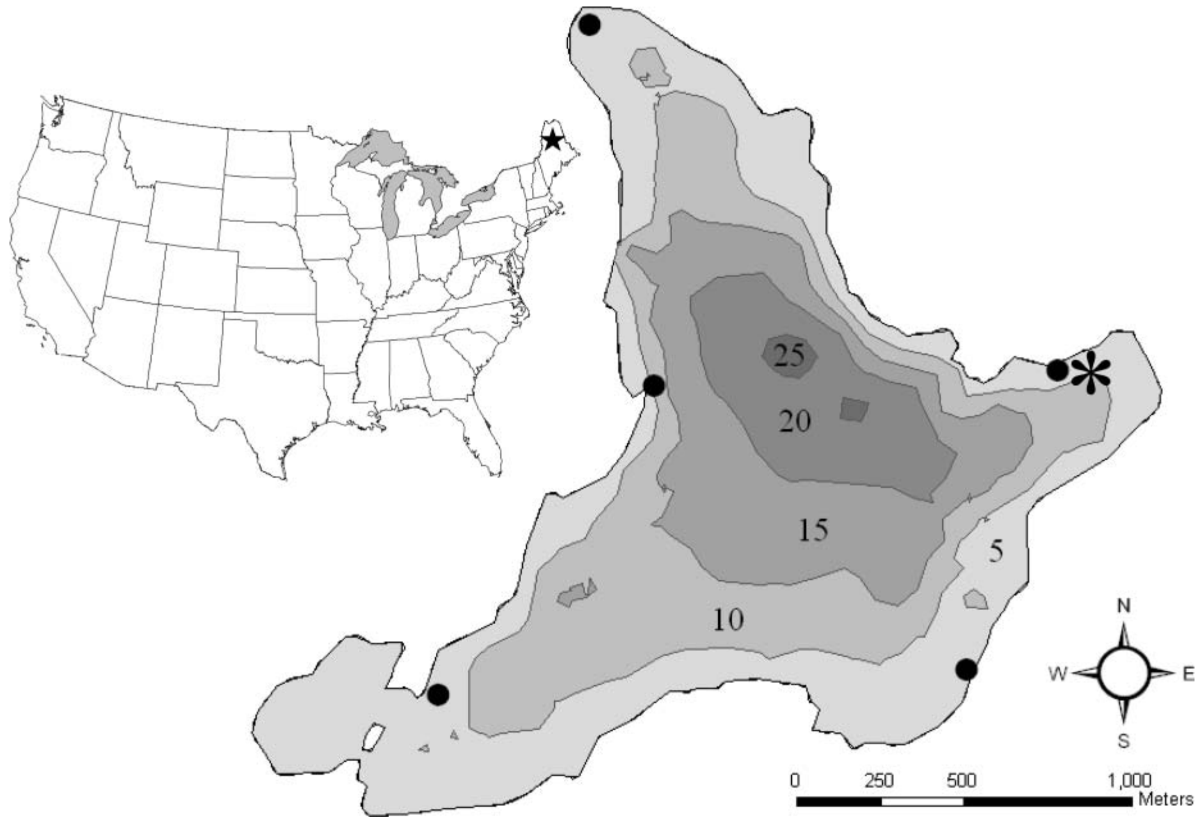

FIGURE 1. Bathymetric map of Clear Lake, with numbers representing depth values as maximum depths (m) for each isocline. Black shaded circles represent locations of each receiver. The asterisk represents the receiver location (Camp Cove) where the water temperature logger was located (inset: star = Clear Lake's location within Maine, USA).

and the time of either sunrise or sunset and then (2) dividing this difference by the length of either the daytime or nighttime period. The values of decimal time ranged from 0 to 1, with sunrise having a value of 0 and sunset having a value of 0.5. Daytime hours ranged from 0.00 to 0.49, and nighttime hours ranged from 0.50 to 0.99. Each day or night period was divided into five bins representing proportions of that period. For example, the first daytime bin included detection events that occurred within the first 20% of the day length, and each subsequent bin likewise represented 20% of the daytime period.

For each detection event, we calculated vertical velocity as the absolute depth change since the last detection divided by the absolute duration between detections. This provided a minimum vertical velocity for each detection event of an individual fish. Data were excluded for fish that were detected less than 10 times within a decimal time bin during a given month. Fewer than 10 detections/decimal time bin were considered to be rare events that were not descriptive enough to represent an individual's behavior. We calculated the median vertical velocity for each fish by year, standard month, and decimal time bin from sunset or sunrise. These medians were finally used to compute the median vertical velocity (m/h) for a given decimal time bin by period and fish. The distribution of vertical velocities was nonnormal; therefore, nonparametric analyses were performed on the data (Shapiro–Wilk test statistic = 0.97, $n = 822$, $P < 0.001$). Diel differences in activity rate by period were analyzed for differences among periods using the nonparametric Kruskal–Wallis ANOVA. Differences between vertical velocities for day and night were compared among periods using Kruskal–Wallis ANOVA. Pairwise comparisons between individual periods were performed by using the Mann–Whitney U-test. All tests were conducted with an α level of 0.05.

Diel habitat use analysis and interpretation.—For each fish, a median depth was calculated for each daytime and nighttime period of each date. These median values were then used to calculate the amplitude by fish and date. The amplitude calculation was the difference between the nighttime median and the daytime median; positive amplitude values represented dates on which nighttime had the shallower median depth, and negative amplitude values represented dates on which daytime had the shallower median depth. These values were further reduced by taking the median amplitude for each fish by month and then within periods. The distribution of median amplitude data deviated from normality, so nonparametric analyses were performed (Shapiro–Wilk test statistic = 0.56, $n = 644$, $P < 0.001$). Fish median amplitude data were analyzed for differences among periods using the nonparametric Kruskal–Wallis ANOVA. Pairwise comparisons between individual periods were performed using the Mann–Whitney *U*-test. An α level of 0.05 was used for all tests.

RESULTS

Tagged Lake Whitefish

Ages of tagged lake whitefish ranged between 3 and 12 years, with most being between 7 and 8 years (Table 1). Fork lengths ranged between 283 and 415 mm. All tagged fish were considered sexually mature based on age, size, and expression of gametes. Observational periods varied depending on tag type; fast-pinging tags had an average of 348 observation days, and tags with lower ping rates had 532 observation days (Table 1). Median daily detection rates for tagged fish were generally high, ranging from 38 to 539 detections/d. Interquartile ranges for these means were also high, suggesting that detection rates were highly variable. Our study observed between 4% and 78% of the theoretical maximum detection rate, with a mean of 25%.

Seasonal Vertical Habitat Use

Lake whitefish from Clear Lake showed seasonal depth distribution patterns that were consistent across all 6 years of data collection (Figure 2B). There was a statistically significant difference in median depths between periods (Kruskal–Wallis ANOVA: test statistic $K = 230.34$, df $= 3$, $P < 0.001$). All four periods showed significant differences with pairwise analysis. During the study, the greatest depths occupied by tagged lake whitefish were observed in the overwinter period. The median depths during this period ranged between 8.1 and 17.7 m, with most fish at or near 15-m depth. During the spring transition, lake whitefish rapidly ascended in the water column and began to occupy depths between 2.4 and 7.2 m; this movement typically occurred over a period of 3 weeks. After spending 2 weeks near the surface, the fish descended to slightly deeper waters. The rate and timing of descent varied between years, but the target depth appeared to be consistent between 8.2 and 13.2 m. Once the fish descended to 8.2–13.2 m, they remained within this depth range throughout summer residency. During fall turnover, lake whitefish once again performed a rapid ascent to shallower waters, after which they maintained a narrow range of shallow median depths between 1.7 and 3.0 m for a period of 5–6 weeks. After fall turnover, the fish descended into deeper waters, where they remained for the duration of overwintering.

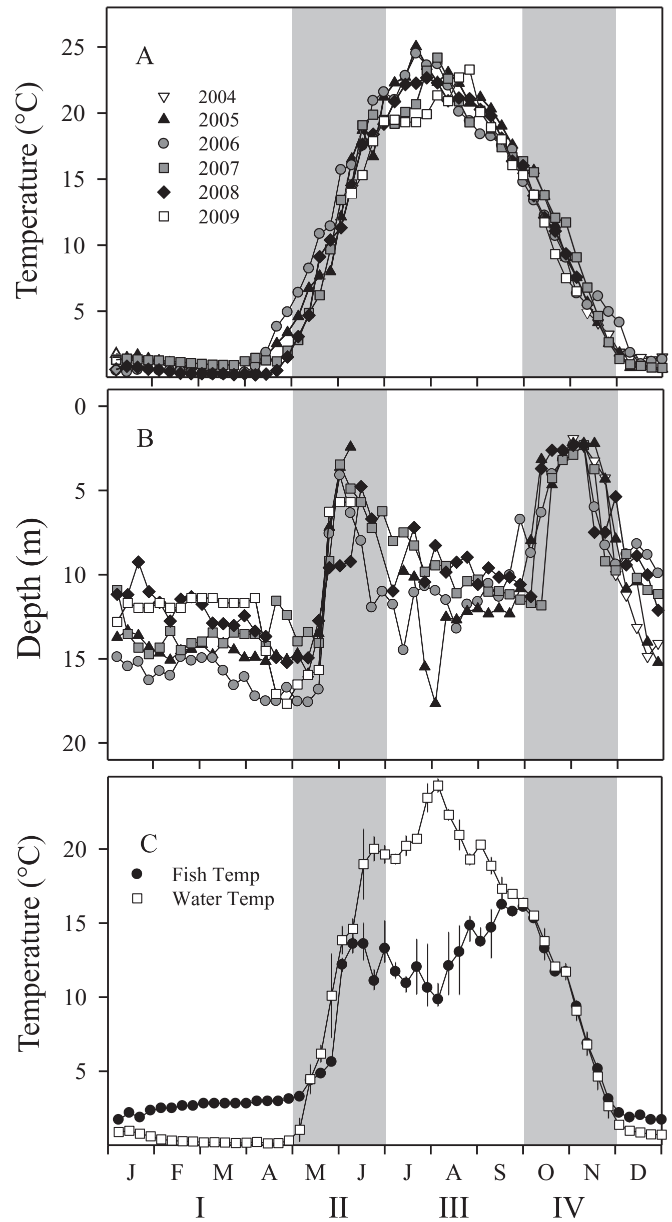

FIGURE 2. **(A)** Weekly mean surface water temperature (°C) in Clear Lake, Maine, by year compiled from data recorded at Camp Cove (Figure 1); **(B)** seasonal vertical distribution of tagged lake whitefish grouped by year (points represent median depth for all tagged fish detected during that standard week); and **(C)** mean weekly surface water temperature (°C ± SE) for 2007 and the corresponding median weekly thermal habitat selection by a tagged lake whitefish. Roman numerals and shading refer to four distinct seasonal periods (I = overwinter; II = spring transition; III = summer residence; IV = fall turnover).

Seasonal Vertical and Thermal Habitat Use

Two lake whitefish received acoustic tags that were equipped with both temperature and depth sensors; detection data from these tags showed behavioral thermoregulation through the selection of vertical habitats with consistent thermal characteristics (Figure 2C). During overwintering, surface temperatures were between 1°C and 2°C. The dual-sensor tags showed that lake whitefish occupied deep waters (12–17 m) where temperatures were higher than those recorded at the surface (2–3°C). Surface temperatures steadily increased during spring transition, and the fish actively followed a thermal gradient such that the temperature at the fish's depth was equal to the surface water temperature. In general, the fish ascended from 16-m depth to 4 m below the surface during this period. When surface water temperatures exceeded 25°C, the tagged fish selected depths where the thermal habitat was between 10°C and 16°C. This thermal habitat was located just below the thermocline at around 9-m depth. When surface water temperatures declined below 17°C during fall turnover, the tagged fish ascended in the water column to depths less than 5 m, where they found thermal habitats that were similar to the surface water temperature. The tagged lake whitefish then followed a thermal gradient back into the vertical and thermal habitats that were observed previously for the overwintering period. Collectively, the vertical movements of the two fish with dual-sensor tags were consistent with those observed for fish with depth sensor tags, suggesting that all of the tagged fish were likewise selecting vertical habitats based on water temperature.

Diel Vertical Migratory Behavior

Tagged lake whitefish exhibited behavioral differences in vertical velocity between daytime and nighttime (Figure 3). Within each seasonal period, tagged fish had significantly higher vertical velocities during daylight hours than during nighttime hours (Table 2). The magnitude and timing of vertical velocity increases were variable among periods. There were significant differences across all periods in both daytime and nighttime vertical velocities (Table 2). Results from pairwise Mann–Whitney U-tests showed that activity levels were significantly different between some periods for both daytime and nighttime vertical velocities (Table 2). Vertical velocities for both daytime and nighttime were lowest during the overwinter period (Figure 3). Vertical velocities during daytime hours ranged from 1.1 m/h in February to 3.1 m/h in December. Nighttime vertical velocities ranged from 0.0 to 1.2 m/h. Vertical velocities for both daytime and nighttime hours increased during the spring transition period, ranging from 1.8 to 6.2 m/h at night and from 3.5 to 9.5 m/h during the day. Sharp peaks in vertical velocity were observed in the intervals immediately after sunrise and before sunset during the month of June. Throughout summer residency, daytime vertical velocities ranged from 2.1 to 6.1 m/h. In August and September, fish exhibited peak activity just before sunset and after sunrise, similar to June observations; nighttime vertical velocities ranged from 0.2 to 4.1 m/h. During the fall turnover period, daytime vertical velocities ranged from 2.5 to 7.6 m/h, and nighttime vertical velocities ranged from 2.2 to 5.1 m/h.

Tagged fish exhibited seasonal differences in diel depth habitats. There were significant differences in the amplitude of depth changes for each diel period across seasonal periods (Kruskal–Wallis ANOVA: $K = 89.45$, df = 3, $P < 0.001$). Fish demonstrated significantly lower amplitudes during the overwinter period than during all other periods (Mann–Whitney $U > 6{,}313$, $n_{\text{I}} = 375$, $n_{\text{II}} = 60$, $n_{\text{III}} = 75$, $n_{\text{IV}} = 134$, $P < 0.003$). Median amplitudes by standard week during period I were very low and not much different from zero (Figure 4A). Period II was not significantly different from period III or IV (Mann–Whitney $U > 2{,}691$, $P > 0.05$), but graphical analysis showed large variability

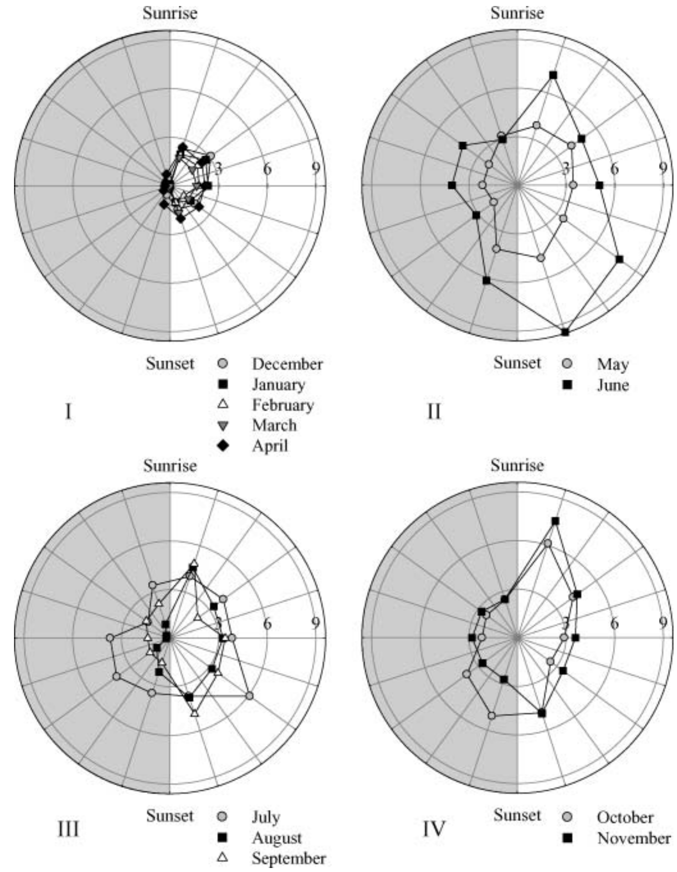

FIGURE 3. Diel vertical migrations of tagged lake whitefish during each period (I–IV; defined in Figure 2). The shaded area on each panel represents nighttime, and the unshaded area represents daytime; each spoke represents 10% of the diel period. Hours are standardized to decimal values between 0.00 (sunrise) and 0.49 for daytime and between 0.50 (sunset) and 0.99 for nighttime. Median vertical velocity (m/h) of all fish is shown on the radial axis.

in the amplitude of depth changes during period II. In the first few weeks of the spring transition period, tagged fish had amplitudes reaching as high as 6.7 m, and these large depth changes occurred as fish moved from deeper daytime depths to shallower nighttime depths. During the second part of the spring transition period, tagged fish actually inverted their behavior and inhabited shallower depths during the daytime, with relatively moderate amplitudes. The amplitude of depth changes during periods III and IV was significantly different (Mann–Whitney $U = 3{,}755$, $P = 0.02$), with the summer period having lower amplitudes. During the summer period, fish tended to occupy shallower depths at night and to display moderate amplitudes, although in some weeks the diel behavior was inverted. Similar to the spring period, the fall transition period for lake whitefish was characterized by shallower nighttime depths and high amplitudes. These observations of the amplitude and direction of depth changes show that during the spring and fall, fish were demonstrating large changes in depth (Figure 4B). During these two periods, the fish typically remained in deeper waters during daytime and

TABLE 2. Results of nonparametric Kruskal–Wallis one-way ANOVAs comparing weekly median vertical velocities of lake whitefish among seasons and between diel periods (sample sizes in parentheses). Results of post hoc Mann–Whitney *U*-tests for differences between paired seasons for each diel period are also presented.

Kruskal–Wallis ANOVA			Pairwise Mann–Whitney *U*-test		
Group factor	Dependent period	*P*	Group factor	Dependent period	*P*
I	Day (500)–Night (494)	<0.001	Day	I–II	<0.001
II	Day (151)–Night (136)	<0.001	Day	I–III	<0.001
III	Day (151)–Night (160)	<0.001	Day	I–IV	<0.001
IV	Day (165)–Night (159)	<0.001	Day	II–III	0.114
			Day	II–IV	0.078
			Day	III–IV	0.936
Day	All (967)	<0.001	Night	I–II	<0.001
Night	All (939)	<0.001	Night	I–III	<0.001
			Night	I–IV	<0.001
			Night	II–III	<0.001
			Night	II–IV	0.415
			Night	III–IV	<0.001

in shallower waters at night. During the winter period, fish did not make significant upward or downward movements between diel periods; in summer, the fish manifested some level of diel depth change but at a much lower magnitude than was observed during the spring and fall periods.

DISCUSSION

Seasonal vertical habitat selection by lake whitefish was strongly linked to the thermal changes in Clear Lake. Lake whitefish actively selected depths where the water temperature was below 16°C, consistent with the documented fundamental thermal niche of 12–15°C (Crowder and Magnuson 1982; Bernatchez and Dodson 1985; Christie and Regier 1988). During the summer period, lake whitefish selected water depths with temperatures between 10°C and 16°C; after stratification, these thermal habitats were located below the thermocline at 9 m. During the stratification period, surface temperatures typically exceeded 20°C. When thermal habitats within the fundamental thermal niche were not available (e.g., during the winter period), lake whitefish selected deep habitats, where they most likely occupied the warmest available thermal habitat. In the spring and fall periods, the fish selected water depths where temperatures matched those recorded at the surface, indicating that these thermal habitats provided the warmest available temperatures, as the water column was either warmer or cooler throughout the period.

Along with temperature, factors such as prey availability, predator avoidance, and the associated metabolic costs can further influence habitat use. The tagged lake whitefish in our study were large enough (>300 mm) to avoid predation by piscivorous fish. Possible predators such as lake trout and brook trout are not likely to consume such large prey. Therefore, the observed behaviors of adult lake whitefish in Clear Lake are probably not influenced by predator avoidance. Conversely, prey availability and the metabolic costs associated with prey encounter and capture are the most likely factors influencing vertical habitat selection by lake whitefish. During the summer period, lake whitefish occupied vertical habitats just below the thermocline; this was likely due to a balance in the metabolic tradeoffs of thermal refuge and prey availability (Gjelland et al. 2004; Kahilainen et al. 2004; Ohlberger et al. 2008). By orienting themselves in the cooler hypolimnion, fish may maintain lower metabolism while also being in a position to take advantage of feeding opportunities in the warmer epilimnion. During the spring and fall, when thermal constraints were released, lake whitefish actively used the surface water habitats where pelagic invertebrate prey were abundant. Likewise, the observed movements in the spring closely followed the emergence of invertebrates that may have been a major food source for lake whitefish during this period. The availability and selection of prey for lake whitefish in Clear Lake are not well studied to date, but linking the observed behaviors and prey selection would increase the knowledge of lake whitefish habitat selection and diet.

Habitat selection in the fall period was probably related to the behavior of spawning fish. Sexually mature adults spawn in shallow shoals or tributaries between late October and November (Anras et al. 1999). Lake whitefish are broadcast spawners and spawn over coarse substrate (from boulders down to gravel) in depths from 2.0 to 4.5 m (Hart 1931; Fudge and Bodaly 1984; Anras et al. 1999). Spawning behaviors typically begin after surface water temperatures fall below 6°C (Hart 1931; Nester and Poe 1984), with intense spawning activity occurring over roughly 1 week (Anras et al. 1999). Although spawning was

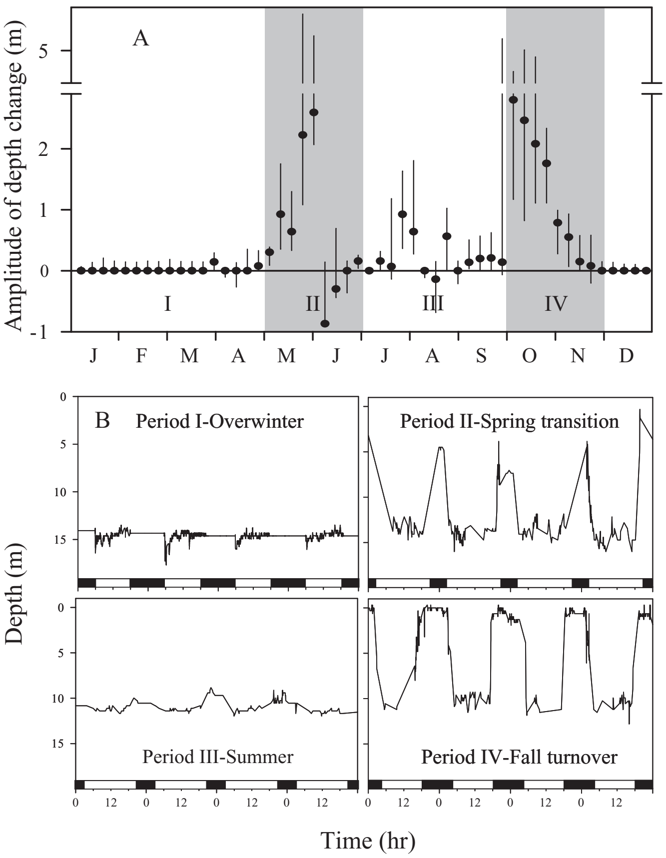

FIGURE 4. **(A)** Median weekly amplitude of depth change for all lake whitefish during each period (represented by roman numerals I–IV and shading). Each point represents the weekly median value of the difference between nighttime and daytime median depths across all fish; error bars represent the 25th and 75th percentiles of median amplitude. **(B)** Representative tracks of individual fish from each period are presented. Each track shows 4 d of typical diel behaviors observed within each period. The bar along the *x*-axis represents the diel cycle (dark = nighttime; white = daytime).

thought to take place at night (Hart 1931), it has recently been suggested that spawning of lake whitefish occurs independent of time or daylight cycles (Anras et al. 1999). In our study, tagged fish were found to occupy depths less than 5 m during October and November. Although spatial detail and spawning fates for tagged fish are unknown, it appears that at least some of the tagged fish were selecting shallow habitats during this period to take part in spawning events.

Lake whitefish activity levels differed between daylight and nighttime hours. It is highly likely that the pattern of vertical movement observed for lake whitefish in our study was associated with feeding behaviors, as was seen in brook trout (Boisclair 1992). The reduction in these activities during the nighttime suggests that lake whitefish are visual predators requiring daylight to detect and capture prey, as has been observed in other coregonids (Link and Edsall 1996; Kahilainen and Østbye 2006; Ohlberger et al. 2008). These activity rates appear to be influenced by both temperature and light conditions (Scherer and Harrison 1988; Nowak and Quinn 2002; Gjelland et al. 2004). Diel differences in activity levels have been observed to change along a seasonal gradient (Gjelland et al. 2004). Daily activity rates of lake whitefish during the daylight hours increased from the overwintering period to the spring transition period as ice coverage decreased and as water temperatures and light penetration increased. Activity levels also showed distinct crepuscular peaks during all periods except winter, suggesting that feeding rates may be higher during the hours immediately after sunrise and before sunset (Gjelland et al. 2004).

Seasonal patterns of diel vertical migration observed in our study suggest that lake whitefish utilize separate vertical habitats for feeding at different times of the year. Similar shifts in habitat use have been observed in other coregonids (Næsje et al. 1991; Kahilainen et al. 2004). These shifts are associated with changes in feeding patterns and prey types from a benthic-dominated prey source to a pelagic prey source. Lake whitefish in Clear Lake appear to follow a pattern of utilizing the benthos during certain seasons and then using the pelagic zone when prey availability there is high. This pattern indicates some amount of seasonal foraging optimization by lake whitefish. The observed diel vertical migration in which fish moved from deep waters during the day to shallow waters at night probably occurred in response to prey selection and prey availability.

The potential impacts of climate change on these observed patterns of lake whitefish behavior and on lake whitefish populations in general are similar to the impacts predicted for many coldwater fish species in North America (De Stasio et al. 1996; Jansen and Hesslein 2004). Because of the strong temperature influence, lake whitefish may migrate up into the surface waters with earlier ice-out dates. These previously food-rich surface waters may not contain abundant prey items unless the life histories of prey likewise evolve to an earlier spring thaw. This could present a temporal mismatch between lake whitefish and their prey, causing lower food availability for and declining condition of lake whitefish. Additionally, water temperatures are hypothesized to increase earlier, thereby causing lake whitefish to have a much shorter window in which to take advantage of the thermal habitats at or near the surface for feeding. This shorter feeding window could also result in declining fish condition prior to summer periods. During these extended summer periods, many fish may lose weight due to high metabolic costs associated with higher water temperatures (Dabrowski 1985). Finally, during the fall, spawning may be delayed, as lake whitefish spawning appears to be highly temperature dependent (Nester and Poe 1984; Anras et al. 1999).

These data demonstrate seasonal variation in habitat use and behavior, which are likely to be driven by temperature during winter and summer and by a combination of temperature and prey availability during spring and fall. Similarly, activity levels and diel vertical migration follow seasonal patterns, as both are driven by temperature in the winter and summer and by a combination of temperature and prey availability during spring and fall. Lake whitefish in Clear Lake have higher activity levels during the day than at night throughout all seasons. Likewise, they perform major diel vertical migration during the spring and fall, which may optimize feeding potential.

Findings from this study are an initial step in relating vertical habitat selection and diel vertical migration behaviors with feeding and spawning. These findings highlight the importance of the timing and variability of environmental conditions for influencing the ecology and behavior of lake whitefish. Future research should focus on understanding prey availability to and prey selection by lake whitefish in each of these seasonal and diel habitats in order to determine the metabolic costs associated with the habitat shifts observed in this study.

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