Depth and Thermal Histories of Adult Sockeye Salmon (*Oncorhynchus nerka*) in Cultus Lake in 2006 and 2007

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DEPTH AND THERMAL HISTORIES OF ADULT SOCKEYE SALMON (*Oncorhynchus nerka*) IN CULTUS LAKE IN 2006 AND 2007

by

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ABSTRACT

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In 2006 and 2007 we tagged adult sockeye salmon (*Oncorhynchus nerka*) entering Cultus Lake, British Columbia to determine their behaviour prior to and during spawning. In both years fish were found at mean depths corresponding to positions below the lake thermocline where the water was 6-8 °C, although we observed a trend towards the use of shallower waters as they matured. There was also some evidence of diel patterns with fish spending nights in shallower and slightly warmer water than during the day. Some fish exhibited an unusual surfacing behaviour prior to death that may have been related to a gill disease that was observed in the population. Only a small fraction of tagged fish appeared to have spawned successfully (14% in 2006, 20% in 2007), suggesting there may have been an impact of tagging on survival.

RÉSUMÉ

Pon, L.B., Tovey, C.P., Bradford, M.J., MacLellan, S.G., and Hume, J.M.B. 2010. Depth and thermal histories of adult sockeye salmon (*Oncorhynchus nerka*) in Cultus Lake in 2006 and 2007. Can. Tech. Rep. Fish. Aquat. Sci. 2867: iii + 39 p.

En 2006 et en 2007, nous avons procédé à une campagne de marquage acoustique des spécimens de saumons rouges adultes (*Oncorhynchus nerka*) entrant dans le lac Cultus (Colombie-Britannique). Cette opération avait pour objet de suivre les déplacements des saumons rouges avant et durant la période de frai. Pour les deux années concernées, on a observé la présence de saumons rouges à des profondeurs moyennes au-dessous de la thermocline (6-8 °C), et une tendance des sujets plus matures à fréquenter les couches d'eau de moindre profondeur. On a également observé des rythmes nycthéméraux caractérisés par des déplacements quotidiens entre « eaux diurnes », plus fraîches et profondes, et « eaux nocturnes », de moindre profondeur et de température plus élevée. Enfin, on a remarqué que certains sujets en fin de cycle vital montaient jusqu'à la surface, comportement qui pourrait être attribué à une pathologie des nageoires observée au sein de la population. Seule une petite proportion des sujets marqués semblait avoir frayé avec succès (14 % en 2006 et 20 % en 2007), dénotant un impact éventuel de l'opération de marquage sur le taux de survie.

INTRODUCTION

The Cultus Lake sockeye salmon (*Oncorhynchus nerka*) stock, one of the most intensively studied populations of salmon in British Columbia (B.C.), has seen a dramatic decline in the abundance of returning adults over the past 40-50 years (Schubert et al. 2002; COSEWIC 2003). Several factors including harvest and predation, poor ocean survival, diseases and parasites, and exposure to warmer temperatures have been identified as contributing to the collapse of the Cultus Lake sockeye stock (Schubert et al. 2002; COSEWIC 2003). In response, Cultus Lake sockeye were listed as endangered by The Committee on the Status of Endangered Wildlife in Canada in 2003 (COSEWIC 2003).

Cultus Lake sockeye are classified as part of the Late-run timing group of Fraser sockeye, which have historically migrated up river in the fall after holding in the Straight of Georgia for up to six weeks (Burgner 1991). In the past, Cultus Lake sockeye salmon arrived at the lake during the period from late September through November, and then subsequently held in the lake until spawning in late November and into December. During this extended period of lake residency, sockeye complete their sexual maturation (Schubert et al. 2002). Since 1995, however, many Late-run sockeye salmon have foregone holding, and instead move into the Fraser River several weeks earlier than they did in the past (Lapointe 2002). Cultus Lake sockeye are no exception to this, and have been entering the lake nearly two months earlier than the historic average (COSEWIC 2003). Coincident with early migration has been a substantial rise in en route and pre-spawning mortality among Late Run stocks; in some years over 90% of the run have perished before spawning (Cooke et al. 2004). Given the scope of this issue, it is important to understand the ecology and behaviour of adult salmon returning to spawning grounds in order to make informed fisheries and conservation management decisions.

Earlier upstream migrations expose salmon to warmer river temperatures, which have been implicated as a mechanism related to high levels of mortality in migrating sockeye salmon (Crossin et al. 2008). However, Cultus Lake may provide a thermal refuge for adults as they complete the final stages of maturation just prior to spawning. Compared with Fraser River temperatures of 15-20 ^{o}C (Patterson et al. 2007), the temperature of the hypolimnion of Cultus Lake is only 6-7 ^{o}C. These cooler waters can reduce the standard metabolic rate of fish, thereby conserving limited energy stores (Farrell et al. 2008), and can also reduce the rate of infection by *Parvicapsula minibicornis*, a parasite that infects most sockeye salmon entering the Fraser River (St. Hilaire et al. 2002). Previous studies have shown that adult salmon can regulate their temperature by selecting cooler locations within a thermally heterogeneous environment (Berman and Quinn 1991; Nielsen et al. 1994). Thermal loggers implanted on sockeye salmon from Lake Washington, USA revealed that fish spent the majority of time in water temperatures ranging from 9-11 ^{o}C (Newell and Quinn 2005). Similarly, telemetry data suggests that the Weaver Creek sockeye, another Fraser River stock in B.C. may take refuge in the depths of Harrison Lake where temperatures are below 6.5 ^{o}C (Farrell et al. 2008; Mathes 2009).

Though research efforts into understanding the life history of this population date back to the 1920’s with the work of R. Foerster and W. Ricker (summarized in Foerster 1968), relatively little is known about the in-lake behaviour, distribution, and thermal exposure of adult fish between the time of lake entry and spawning (Schubert et al. 2002). In order to address this information gap, adult sockeye returning to Cultus Lake in 2006 and 2007 were fitted with intra-gastric acoustic tags equipped with depth sensors, and tracked throughout their residency in Cultus Lake. Thermal depth profiles of Cultus Lake were matched with the recorded depths of sockeye in order to estimate their thermal histories. These data were analysed in order to address the following objectives: (i) to examine in detail the depth and thermal behaviour of sockeye salmon within the lake, including temporal trends, (ii) to identify potential locations used for spawning, and (iii) to examine the relationship between lake entry timing and pre-spawning mortality.

METHODS

STUDY AREA AND SPECIES

Cultus Lake (49^{o}03'N, 121^{o}59'W) is a relatively small lake (6.3 km^2) located approximately 90 km east of Vancouver, British Columbia (112 km east of Fraser outlet). The lake sits at an elevation of 43 m. The lake basin is characterised by steep sides and a flat bottom, resulting in a relatively small littoral area (12%; COSEWIC 2003; Fig. 1). Though classified as oligotrophic, Cultus Lake has a relatively high rate of productivity and is considered nutrient limited (Schubert et al. 2002). The maximum depth of Cultus Lake is 42 m, and the mean depth is 31 m (Ricker 1952). Cultus Lake is drained at the North end by Sweltzer Creek, which flows to the Vedder River, and then to the Fraser River. The Cultus drainage basin is 56 km^2.

Cultus sockeye exhibit a strong 4 year generational cycle, with a dominant cycle, a subdominant cycle, and two relatively weaker cycles. These cycles are largely maintained by the tendency of fish to mature at four years. Maturing fish return to Cultus Lake after approximately 2.5 years at sea and spawn from late November through December (Foerster 1968). Spawning has historically occurred at several locations around the lake, though more recently it was thought to be limited to the foreshore at Lindell Beach, despite none having been observed there in recent years (Schubert et al. 2002; Fig. 1). Other known spawning locations are Honeymoon Bay and Spring Bay (Fig. 1). While it was previously thought that Cultus sockeye spawn at depths to 6 m (Schubert et al. 2002), recent work using an underwater ROV has shown that fish may spawn at depths up to 20 m (S. Grant personal communications). Due to their decline, efforts to recover the Cultus Lake sockeye stock include a captive broodstock program, and active predator control.

TAGGING

We conducted a two year investigation into the depth and thermal history of adult Cultus Lake sockeye using acoustic tags equipped with depth sensors. All fish were tagged prior to entering the lake, and the depth history of in-lake fish were recorded by an array of acoustic receivers. Lake temperature profiles were associated with individual depth records and the thermal histories of fish were determined.

Between 3 October and 2 November, 2006, 15 sockeye salmon were captured by dipnet at an enumeration fence located on Sweltzer Creek, near the outlet of Cultus Lake. Immediately following capture, fish were placed in a v-shaped trough filled with river water. An acoustic tag equipped with a pressure sensor (2006: V16P-1L; 2007: V13P-1L; both Vemco Inc., Halifax, Canada) was inserted through the mouth of fish and pushed into the stomach with a blunt, rubber-tipped inserter. Tags used in 2006 measured 16 mm by 54 mm and weighed 20 g in air (9 g in water) and in 2007 measured 13 mm by 36 mm and weighed 11 g in air (6 g in water). Sex was determined using visual indicators, and a fin punch was taken for DNA analysis. A Peterson disk tag was attached to the dorsal fin musculature for external identification purposes. Female fish were preferentially captured, although some males were tagged as well. The above procedures were repeated in 2007 on 20 fish between 13 August and 26 October. In both years, capture and tagging occurred at approximately 09:00. No anaesthetic was used during the tagging procedure. In 2006 tagged fish were released upstream of the enumeration fence on Sweltzer Creek, and allowed to recover and move into Cultus Lake on their own. However in 2007 tagged fish were placed in a transportation tank and were released directly into the lake at Main Beach at the northern end of the lake.

In 2006, tags were set to give off a signal on average every 17.5 seconds, though the interval between signals could vary from 5 to 30 seconds. However, not all transmitted signals were received and recorded because concurrent signals could produce collisions, which were not decipherable by the receivers (Voegeli et al. 1998). The frequency of collisions was related to the number of tags and the frequency with which tags emitted a signal (Simpfendorfer et al. 2008). In 2006, nearly two-thirds of all signals recorded were erroneous.

Because 2006 was the first year that Cultus Lake sockeye were tagged with acoustic transmitters, several changes were made to improve the subsequent effort in 2007. These included the tagging of a greater number of fish, an earlier initial tagging date, and a reduction in the frequency of signal transmissions from 17.5 sec to 30 sec. The latter was thought to help reduce the number of collisions between tags, as there were more sockeye tagged in this year than in 2006, and acoustically tagged northern pikeminnow (*Ptychocheilus oregonensis*) were also present within Cultus Lake.

ACOUSTIC RECEIVER ARRAY

Eight receivers (VR2 model, Vemco Inc., Halifax, Canada) were deployed in Cultus Lake in an arrangement that covered the vast majority of the lake (Fig. 1). The effective detection range of receivers ranged from 1280 m to 2110 m based on a previous study (C. Tovey, Unpublished data) and no receiver was more than 1.25 km from its nearest neighbour. Due to the extent of the detection range, and the spacing of the receivers, substantial overlap among receivers was present, meaning that in most locations, except along some shorelines, a tag could be simultaneously detected by multiple receivers (Fig. 1).

Receivers were submerged in the lake, at locations approximately 140 m offshore. Receivers were attached to a line weighted at one end, and a small buoy attached to the other end. This method of deployment held the receiver upright within the water column at approximately 2 m from the lake bottom. A leaded-line was attached to the weight and ran to shore where it was anchored to a brick, which enabled receiver retrieval. This allowed for retrieval of the receiver for downloading the data records. Data was recovered from the receivers several times during the field studies to avoid reaching the maximum memory capacity of the devices. For 2006 data, receivers were downloaded on 2, 3 November and again on 22, 24 January 2007. For 2007 data, receivers were downloaded 10, 12 October, 28, 29 November, and 16, 17, 21 January 2008. Receivers were replaced at the same location using GPS coordinates.

DATA LOSS

Despite downloading data from receivers several times throughout the study periods, there was still some loss of data. Specifically, VR2 7648 (Station G) ceased recording transmissions on 23 October after 19:43. The receiver was reinitialised and redeployed on 3 November. VR2 7644 (Station B) ceased working from 27 November 06:46, as did VR2 7646 (Station F) from 6 November 18:37, and VR2 7642 (Station H) from 26 November 05:07. These receivers did not record data through 24 January 2007. The consequence of data loss from non-functional receivers was abated in part by the redundancy of overlap among the eight receivers deployed in the lake. However, during the periods that receivers were not functioning, it became more difficult to identify the general area in which fish were spawning. In particular, loss of data from the VR2 located at near Spring Bay and Honeymoon Bay (Station F) may have precluded or increased uncertainty in identifying potential spawning locations. Receiver failures were due to a software fault that was rectified for the 2007 study period.

LOCATING TAGS

Due to the large radius of detection of receivers, it was not possible to pinpoint the locations of tags with a high degree of accuracy. Instead, manual hydro-acoustic surveys were conducted using a portable receiver (VR100 model, Vemco Inc., Halifax, Canada). For the 2006 study, tags were located to within approximately 15 m of the actual position by using a directional hydrophone attachment for the VR100. The 2007 study was limited to the use of location estimates obtained from grid surveys, which were conducted from a boat and along pre-defined transects. Unlike the VR2 receivers which do not record signal strength, the strength of the signal picked up by the VR100 can be used to estimate the distance the tag is from the receiver. An omnidirectional hydrophone attachment for the VR100 was used to obtain multiple location records from tags. By weighting the UTM locations of the grid points by the number of detections per unit of time at that point, we were able to determine the location of tags to within approximately 300 m of the actual position.

Surveys for the 2006 and 2007 studies were conducted 1 February, 2007, and 9 January 2008 respectively. In both cases, surveys were conducted after all tagged fish had died. Thus, tag locations determined from the surveys likely represent the general area of the lake that fish occupied just prior to death. The tag locations estimated from the manually conducted surveys were checked against VR2 records corresponding to the final detections made for each fish just prior to death.

POTENTIAL SPAWNING EVENTS

Although it is impossible to determine which fish successfully spawned from the receiver data alone, there are several observations, that when taken together, indicate a potential spawning event for some fish. These criteria included an extended stay at a particular depth, consistent with what would be expected from territorial behaviour associated with spawning site selection and egg protection (Foote 1990). The second criterion was that the tag be consistently detected by one or more receivers during the time frame corresponding to spawning. The third was that the depth be less than 20 m; a previously identified maximum spawning depth in Cultus Lake. Fourth, a mortality event (e.g. the continual recording of a tag at its final depth) was expected to occur shortly following the identified spawning event. Finally, we only examined cases in which this occurred following early November as this timeframe corresponded roughly with the time when Cultus sockeye taken from the fence for the captive broodstock program became fully mature. These criteria were assessed only for female fish. Potential spawning sites were estimated from the locations determined by manual surveys. These locations were checked to see if they were within the range of the specific VR2s on which fish were recorded during the spawning event.

DATA ANALYSIS

As there were other acoustic tags in Cultus Lake unrelated to this study (e.g. northern pikeminnow), data records downloaded from the VR2 receiver array were filtered to remove non-relevant transmissions, as well as errors resulting from problems associated with signal collisions. We collected 3.5 million data points that were specific to the study fish. All data were standardised to Pacific Standard Time, and compressed into more manageable formats by averaging depth records from individual fish over consecutive 15 minute intervals throughout the period of time for which each fish was detected within the lake. All further analyses were conducted using this reduced dataset.

Water temperatures were obtained from the casts a conductivity temperature depth (CTD) meter (model STD-12 Plus or Micro CTD Sensor, Applied Microsystems, Sidney, B.C., Canada). Temperatures were measured on 5, 13, and 16 October, 2, 7, 17, and 22 November, and 6 December of 2006 and 9, 22 August, 27 September, 17 October, 14, 21, 26 November, and 5 December of 2007. Data for days between CTD casts were estimated by interpolation. Daily water temperatures were associated with depth and added to the database of tag detections downloaded from the receivers. Potential relationships between depth and time were analysed using linear regression analysis. Fish 140 was removed from the 2006 dataset for this analysis as it was only detected in the lake for four days before disappearing.

To examine diel patterns in depth and thermal exposure, civil twilight was used to differentiate between day and night. Data for the daily beginning and ending of civil twilight for the periods corresponding to when tagged fish were alive was acquired from the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Individual depth and temperature data points were assigned to either day or night for all recordings produced by the quarter-hour mean compression. Student’s paired t-tests were used to compare the mean night and day depths and temperatures for all individuals within each year. Similarly, the coefficient of variation in depth and thermal history were compared among day and night recordings using student’s paired t-tests.

To examine the relationship between lake entry timing and survival, multiple regression analysis was performed. Survival was calculated from 1 November so as to include all release dates. Two fish (148 and 164) did not survive until November, and were excluded from the regression analysis. All statistical tests were assessed for significance at an alpha level of 0.05 using SAS v9.1.

RESULTS

Of 15 fish tagged in 2006, 11 were females, three were males, and for one, sex was undetermined. All but one fish (#144) were detected in the lake, although fish #143 was only detected for a week before disappearing from the array. Of the 20 fish tagged in 2007, 16 were females, and four were males. All fish in this year were detected in the lake. Several fish disappeared part way through the study period in 2007, though these fish may have been washed ashore following death. One fish (#165) was found 3km downstream of the lake at the confluence of Sweltzer Creek and the Vedder River. The remaining fish in both years were tracked throughout their residency in Cultus Lake. Collectively, these records revealed a depth history profile for each fish, which were matched to the corresponding temperatures at depths to develop individual thermal exposure histories. Details of tagging data in 2006 and 2007 are presented in Tables 1 and 2 respectively.

LAKE TEMPERATURE DATA

The lake remained stratified until approximately mid-November in both years (Figs. 2 and 3). During this time, the thermocline depth was between 10 m and 15 m. In 2006, mean water temperature in the epilimnion was 13.3 ^{o}C (range 9.4 ^{o}C – 17.7 ^{o}C) and 6.3 ^{o}C in the hypolimnion (range: 6.0 ^{o}C – 8.5 ^{o}C). As the 2007 study period began sooner in the year, mean water temperature in the epilimnion was 15.3 ^{o}C (range 20.8 ^{o}C – 9.4 ^{o}C) and 6.2 ^{o}C in the hypolimnion (range: 5.8 ^{o}C – 8.3 ^{o}C).

DEPTH AND THERMAL EXPOSURE

In 2006 when fish were released in Sweltzer Creek they typically were detected in the lake within 24 hrs. The complete depth histories of individual fish in 2006 and 2007 are detailed in figures 4 and 5 respectively. Mean individual depths and the corresponding temperatures are presented in tables 3 and 4. Taken together, fish in 2006 were found at a mean depth of 17.5 m (SD = 8.11, range = 0 – 40.6) and a corresponding mean temperature of 7.98 ^{o}C (SD = 2.18, range = 5.9 – 17.54). The distribution of depths that fish were recorded at in 2006 was bi-modal, with one peak below the thermocline, and another in shallow water (< 2.5 m; Fig. 6A). Fish spent most time at depths below the thermocline early in lake residence, and occupied shallower waters late in the year when the lake was nearly mixed. As a result, the thermal distribution of records is heavily skewed towards cooler temperatures (Fig. 6C).

In 2007, fish were found at a mean depth of 19.2 m (SD = 8.42, range = 0 – 41.8) and a corresponding mean temperature of 7.37 ^{o}C (SD = 1.50, range = 5.81 – 20.80). The distribution of depth records was similar to that of 2006, with one peak below the thermocline, and another in shallow water, which likely corresponded to spawning as depth records after 15 November were much shallower (Fig. 6B). The distribution of thermal records was also similar to 2006; heavily skewed to lower temperatures (Fig. 6D).

Although limited in terms of sample sizes, no differences in mean depth were apparent among males and females 2006 (Wilcoxon Kruskal-Wallis test; χ^2 = 1.029; P = 0.311). A marginally significant difference in mean temperature was detected however, with males being in slightly cooler water (Wilcoxon Kruskal-Wallis test; χ^2 = 4.114; P = 0.043). In 2007, no difference was found in mean depth (Wilcoxon Kruskal-Wallis test; χ^2 = 0.723; P = 0.395), nor mean temperature (Wilcoxon Kruskal-Wallis test; χ^2 = 1.509; P = 0.219) among males and females.

DEPTH AND THERMAL TRENDS

Fish tended to move to shallower waters as the time spent in the lake progressed. In 2006, the data were well described by a sinusoidal curve, and the regression of depth and date was highly significant (day: R^2 = 0.95; P < 0.001, night: R^2 = 0.94; P < 0.001; Fig. 7A). The move to shallower waters in 2006 resulted in a trend to exposure to warmer waters over time (day: R^2 = 0.85; P < 0.001, night: R^2 = 0.77; P < 0.001; Fig. 8A).

A number of fish in 2006 showed a pronounced surfacing behaviour prior to their apparent death prior to spawning (e.g., #132, #138, #141, and #142). In these cases fish moved from the hypolimnion to the surface before descending to the bottom after death. The time spent on the surface was usually only 1-2 days.

The 2007 dataset was slightly more complex as it spanned a greater period of time, including late August and the month of September. Furthermore, there was an influx of newly tagged fish over an extended period of time which may have increased the variation in depth and temperature on days when new fish were introduced to the lake (Table 2). The 2007 data were well described by a quadratic regression curve with fish initially trending towards deeper water up until late September, when the trend reversed, and fish moved progressively into shallower water (day: R^2 = 0.64; P < 0.001, night: R^2 = 0.70; P < 0.001; Fig. 7B). These trends were reflected in the temperatures that fish were exposed to over the study period; initially moving to cooler water, and then towards warmer water (day: R^2 = 0.75; P < 0.001, night: R^2 = 0.82; P < 0.001; Fig. 8B). Although fish identified as potential spawners generally moved to shallow waters, we also observed a similar surfacing behaviour among many other fish just prior to death (e.g. 2006, fish #134, #138, #139; 2007, fish #147, #150, #152, #157; Figs. 4 and 5).

DIEL PATTERNS

In both years, sockeye tended to spend nights in shallower and warmer waters (Figs. 7 and 8). In 2007, mean water depth during the day was 1.84 (0.31) m deeper than night (paired t-test; t = 6.3; P < 0.001), and mean temperature was 0.25 (0.04) ^{o}C cooler (paired t-test; t = 6.0; P < 0.001). Similar trends were present for 2006, though the effect size was less pronounced; mean water depth during the day was 0.93 (0.38) m deeper than night (paired t-test; t = 2.5; P = 0.029), and mean temperature was 0.40 (0.18) ^{o}C cooler (paired t-test; t = 2.4; P = 0.032). Mean day and night depths and temperatures for individuals are summarized in Tables 3 and 4. Interestingly, a larger diel difference in mean temperature was observed in 2006 than in 2007 despite a smaller difference in mean depth. This is likely due to the fact that the 2007 study period was initiated earlier in the year, and hence captured a greater range of fish behaviour than the study in 2006.

No difference was detected in the variability of thermal exposure between night and day in 2006 (CV_{day} = 20.96, CV_{night} = 22.67; paired t-test; t = -1.5; P = 0.169) nor in 2007 (CV_{day} = 19.70, CV_{night} = 19.28; paired t-test; t = 0.7; P = 0.516). However, a difference was detected in the variability of depth between night and day for 2006 (CV_{day} = 40.73, CV_{night} = 51.20; paired t-test; t = -2.2; P = 0.044) and for 2007 (CV_{day} = 42.04, CV_{night} = 46.59; paired t-test; t = -5.0; P < 0.001). These observations may be due to the fact that some fish were observed to hold stationary in shallower water generally during periods of night, while more vertical movements occurred during the day (e.g. fish #149 and #150; Fig. 9). These movement patterns were more evident in the early stage of the 2007 study and less so in the later stages of lake residency for these fish (Fig. 7B).

LOCATIONS AND POTENTIAL SPAWNING EVENTS

Final locations of tags located from manual tracking surveys conducted for the 2006 and 2007 studies are presented in figures 10 and 11 respectively. In 2006, fish carcasses were fairly evenly distributed throughout the lake. Few fish were located in shallow waters, with most at depths between 30 and 40 m. In 2007, carcasses were slightly more concentrated in the southern part of the lake, and most were found in deeper waters. In both years, tag locations determined from the manual surveys were consistent with records from receivers leading up to the time of death, although the locations provided by receiver records were very broad due to the wide range of detection. Nevertheless, this observation suggests that following death, fish carcasses are likely to stay within the same general area.

In 2006, two fish (#135 and #137) were identified as having possibly spawned based on the criteria described above (Fig. 4). Fish #135 was deemed to have potentially spawned in waters shallower than 2 m between 3 and 7 November and to have died shortly thereafter. During this time frame, the signal was detected within the intersection of receivers E, G, and H, suggesting that spawning took place at some location in the southern part of Cultus Lake. From the manual survey, fish #135 was located off the southeast shore between Honeymoon Bay and Maple Bay suggesting that the fish likely spawned along this section of the shore (Fig. 10). The established criteria indicate that fish #137 may have spawned at a depth of 3 m between 17 and 28 November. During this period of time, this fish was consistently detected within the intersection of receivers B and C. From the manual survey this tag was detected c. 500 m offshore from Honeymoon Bay, suggesting that this fish may have moved off of the spawning site prior to death (Fig. 10).

Four fish (#149, #151, #154, and #159) were determined to have potentially spawned in 2007 using the established criteria. Fish #149 appeared to have spawned at a depth of 10 m between 13 and 19 November (Fig. 5). During this time, the fish was detected by receivers E and F, placing the fish somewhere in the central part of the lake. From the grid survey, the tag was located in Mallard Bay close to receiver C, suggesting that the fish likely drifted here after spawning in the intersection of receivers E and F (Fig. 11). Fish #151 was determined to have possibly spawned at a depth of 3.5 m between 15 and 19 November. The fish was detected by receivers F and D during this period, placing it along the shore near Jade Bay. The grid survey however, found the tag further south in the vicinity of receiver H, suggesting that the fish may have left the spawning site prior to death (Fig. 11). Fish #154 was thought to have spawned at a depth of 17 m between 21 November and 1 December at a location where receivers E and F intersected. The grid survey found the tag along the southeast shore, near receiver H, suggesting that the fish may have spawned at a location nearby (Fig. 11). Fish #159 was thought to have spawned at a depth of 2 m between 9 and 30 November. This period corresponded to detections by receivers F, D suggesting that spawning may have occurred along the east coast. The grid survey located the tag within this range in Honeymoon Bay, suggesting a potential spawn site along this section of the lake (Fig. 11).

MISSING TAGS

In 2006, only fish #143 was unaccounted from the manual survey, but this was expected as the fish had only been recorded in the lake for approximately one week before disappearing 23 October. Several tags could not be found during the grid survey conducted in 2007. Both fish #153 and fish #165 disappeared during the study period after moving towards the surface on 14 November, and 4 December respectively. Tag #165 was subsequently detected in Sweltzer Creek near the Vedder River. Tags from fish #152 and #163 were not present during the grid survey, although acoustic records show that these fish died in the lake on 7 November (fish #152), and sometime between 25 October and 13 November (fish #163). Acoustic recordings indicate that both fish died, and sunk to the bottom (Fig. 5), suggesting that the tags may have ceased working at some time prior to the grid survey (9 January, 2008).

LAKE ENTRY TIMING AND SURVIVAL (2007)

In 2007 we found a significant polynomial relationship between the date of lake entry and the time alive after 1 November (R^2 = 0.445, P = 0.012; figure 12). Fish that entered the lake in mid September tended to outlive those from earlier entry dates, as well as those from later entry dates. Due to the limited number of tagging dates in 2006, we are unable to analyse the data in a similar manner, nor compare the data among years.

DISCUSSION

The data presented here represents the first detailed examination of the adult lake residency phase of the life history of Cultus Lake sockeye salmon. The objectives laid out for this study were met with varying degrees of success. In terms of examining the depth and thermal behaviour of sockeye salmon within the lake, we were able to record a highly detailed history of in-lake behaviour from which we observed vertical movement trends at a diel scale as well as a larger scale encompassing the study period. In terms of locating potential spawning locations, we were somewhat limited by the capabilities of the telemetry system that was used. The wide detection range of individual receivers made it impossible to pinpoint the specific location of fish while they were still alive. Tag location using the VR100 was more accurate, but was limited to manual surveys that were conducted largely after fish had already died. Nevertheless, we were able to approximate the potential spawning locations for several fish. In examining the relationship between lake entry timing and survival, we were limited to using the 2007 dataset, but were able to detect a quadratic relationship with poor survival for fish entering the lake both early and late. An intermediate entry date was related to greater longevity of fish.

PRE-SPAWNING DEPTH AND THERMAL BEHAVIOUR

In both years, fish were largely found at temperatures below 8 ^{o}C, which corresponded to depths below the thermocline (i.e., > 15 m depth). The selection of a relatively cooler thermal environment amongst a range of available temperatures is not surprising, and has previously been identified as a behavioural strategy among migrant adult salmon (Berman and Quinn 1991; Hodgson and Quinn 2002; Newell and Quinn 2005; Farrell et al. 2008). This behaviour can reduce the metabolic demand placed on fish, and thereby conserve limited energy stores (Berman and Quinn 1991). However, the abnormally early river entry timing of recent years may negate this advantage as fish spend longer periods of time in freshwater environments (Cooke et al. 2004). In contrast to other Fraser River stocks, adult Cultus Lake sockeye spend an unusually long period of time in freshwater environments prior to spawning. This behaviour is likely made possible by the availability of a thermal refuge from warm river temperatures. However, to say that Cultus Lake sockeye use the lake as a thermal refuge is somewhat misleading as the lake environment coincides with their spawning grounds. Nevertheless, by holding in the cool depths of the lake just prior to spawning, sockeye are able to minimise their thermal exposure during the final stages of sexual maturation; a behaviour which may reduce the rate of pre-spawning mortality (Farrell et al. 2008).

From the depth and temperature records, we detected two behavioural trends. The first, a progressive shift towards warmer and shallower waters was observed in 2006 and the latter part of the protracted 2007 study period. Though figures 7A and 7B show a continuous movement toward shallower water, it should be reiterated that these trends are based on the mean depths taken from all tagged fish on a given day. It was not the case of all fish moving to shallower waters en mass, but rather the increasingly prevalent movement of individuals to shallow waters over a period of time. Nevertheless, many individuals followed this behavioural trend, and were recorded near the surface in the time just prior to death. The cause of this behaviour may have been related to one of several possibilities.

Approaching maturation, spawners could be expected to seek out potential spawning territories, which would generally correspond with shallower sites within the lake where fish are known to spawn. At this time water temperatures in the epilimnion of the lake were more favourable to fish as the lake continued to mix in late October and November. For other fish, this behavioural trend may be related to infection, since many fish did not spawn, but still demonstrated a movement to shallow waters before dying. Many Cultus sockeye captured in 2006 and 2007 were found to be suffering from severe gill hyperplasia associated with *Parvicapsula* infection, which would limit their ability to uptake oxygen (Bradford et al. 2009). This disease appeared to stimulate the movement to the lake's surface probably to allow air breathing to compensate for the loss of gill function (Meakins and Walkey 1975; Barber et al. 2000).

A further complication in Cultus Lake is the recently observed decrease in O_2 concentrations in the deeper limnetic waters during the fall months before turnover (Shortreed 2007). In 1927-1935 O_2 at 30 m ranged from 11 to 9 mg/L from September to December (Ricker 1937). In 2002-2003 O_2 at 30 m was considerably lower, ranging from 8 to 6 mg/L and steadily decreased throughout the fall and early winter (Shortreed 2007). In 2008 the depth of the 8.0 mg O_2/L isopleth rose from 28 m in July to 18 m in November and December (DFO, unpublished data). It is possible that as the deeper waters became progressively more O_2 depleted throughout the fall, sockeye avoided lower O_2 concentrations by holding higher in the water column. Meakins and Walkey (1975) also suggest that vertical distribution may be affected by fish seeking more oxygen rich water. Davis (1975) determined that most salmonids in freshwater would not be affected by O_2 concentrations > 7.75 mg/L, while at 6.0 mg/L most members of a population would start to exhibit symptoms of oxygen distress. Oxygen concentrations in the deeper waters of Cultus Lake appear to be in a range that may cause noticeable stress in some prespawn sockeye particularly if already stressed from a disease such as severe gill hyperplasia.

DIEL PATTERNS

The second trend we observed among fish occurred at diel time scale. Generally, studies that report diel patterns among other fish species largely attribute the behaviour to predator and prey relationships; juvenile sockeye salmon are no exception (Clark and Levy 1988; Schubert et al. 2002). Adult Pacific salmon, however, cease feeding prior to freshwater entry (Groot and Margolis 1991), and adult sockeye in Cultus Lake have few if any predation threats. Therefore, an explanation for diel changes in depth may be more difficult to identify, particularly as few studies have previously looked for such trends in adult salmon, and those that have reported varying results. Sockeye salmon in Lake Washington, USA, showed no diel variation (Newell and Quinn 2005), while sockeye in Harrison Lake, B.C. were found to make a foray to the surface at night, while generally remaining at depth during the day (Mathes 2009). We found Cultus Lake sockeye at shallower depths at night, and deeper depths during the day in both years of the study. However, when using civil twilight to distinguish between day and night, the difference we observed in depth between the two periods was only within 2 m. This is likely due to several factors associated with the depth behaviour exhibited by fish over the course of the study period.

Although many fish demonstrated a cyclical change in depth that roughly corresponded to a diel time scale (e.g. Fish #149, #150; Fig. 9), this trend was not always apparent, nor was it consistent within a given timeframe from fish to fish. While most fish appeared to ‘rest’ while holding at a consistent depth during the night, others (e.g. #155, #160) demonstrated this behaviour during the day. While this trend was particularly evident among fish tagged in the early stages of the 2007 study period, it became less prominent as spawning time approached and the lake mixed. Several fish tagged later in the season did not display the same behavioural trend at all. In fact, the only consistent observation of this behaviour among fish was that the period of ‘rest’ occurred at relatively shallower depths than other times. The cause of this behaviour remains elusive and to our knowledge has not been previously described in adult Pacific salmon. Newell and Quinn (2005) observed that maturing salmon in Lake Washington did not select the deepest (i.e. coolest) available habitat, and speculated that this may have been related to a tradeoff between minimising metabolic costs while not restricting the continuance of sexual maturation. This may partially explain what we observed among Cultus Lake sockeye, but does not rationalise why periods of apparent rest were conducted in slightly warmer waters. Furthermore, Cultus sockeye used in the captive broodstock program reached full maturity in lake water taken from the hypolimnion, suggesting that this thermal range was suitable for sexual maturation.

SPAWNING LOCATIONS

From manual survey data, we can infer that fish were fairly well distributed throughout the lake. However, as many fish appeared to experience pre-spawning mortality, we are unable to determine whether this broad distribution would contract as spawning commenced, although this may be likely as fish move towards viable spawning locations within the lake. A major assumption we must address in regard to identifying spawning sites is that the locations determined from the surveys were indeed representative of where fish spawned. Because female sockeye salmon typically defend their redds until they die (Burgner 1991), it may be reasonable to assume that the final location of the tag from identified spawners should be within close proximity to the spawning location. However, since carcasses were often detected at depths much greater than that which they were thought to spawn at, we cannot ignore the possibility that fish may have moved away from their redds prior to death. Although carcasses may resurface due to bloating (e.g. fish #148; Fig. 5), and can be further dispersed by wind and surface currents before sinking again, we did not observe this in any of the potential spawners prior to the dates when surveys were conducted. Nevertheless, this may simply be the carcass sinking to the lake bottom, down the relatively steep slopes of the lake. Further evidence supporting this comes from the fact that locations determined from the surveys placed carcasses within range of the receivers on which fish were detected during the period of time corresponding to spawning events.

From our data, we can surmise that fish spawned at several locations throughout the lake. Previous work has identified Lindell Beach as an important spawning site; although fewer fish have been sighted there in recent years (Schubert et al. 2002). None of the fish that were thought to have spawned in either 2006 or 2007 were detected at this site. One potential spawner, fish #149, was located post mortem near Mallard Bay, another historically known spawning locale (Foerster 1929). Though not detected by the nearest receiver (i.e. receiver C), other receiver detections suggest that it was plausible that fish #149 may have been in Mallard Bay when it was thought to have spawned.

The recorded depth history of other fish deemed to have potentially spawned also contained occasional detections by other receivers throughout the spawning period. Though this may suggest that fish are moving around, it may also be attributable to the fact that spawning events may be obscured from detection by lake-bottom topography, which can block acoustic signals (Simpfendorfer et al. 2008). For example, fish #163 (tagged in 2007) was recorded moving towards shallow waters in late October, and thereafter detected on rare occasion at <3 m for two weeks before descending to depth in a manner consistent with a sinking carcass (Fig. 5). Though this behaviour may have been consistent with spawning, we did not include this fish as such due to the lack of recorded data during this period of time. Similarly, fish 135 (tagged in

2006), which was thought to have spawned, was still alive when the grid survey was conducted in 2006. Though the survey placed the fish near Honeymoon Bay, the fish was not detected during this time on the nearest receiver (receiver H).

It should also be noted that locations were based on the assumption that no transmitters were expelled from fish prior to death. Understandably, the recordings of a regurgitated transmitter sinking to the bottom of the lake may be similar to those we presumably observed from fish. However, the rapid descent of a fish following death is consistent with other observations of salmon mortalities in lakes (Mathes 2009). Furthermore, while we acknowledge the possibility that tag regurgitation occurred during the study period, other studies have generally reported low (<2%) tag expulsion rates in adult Pacific salmon (e.g. Ramstad and Woody 2003; Cooke et al. 2005; Naughton et al. 2005).

LAKE ENTRY AND SURVIVAL

Many of the tagged fish appeared to suffer from pre-spawn mortality. In fact, only 14% of fish tagged in 2006 and 20% of fish tagged in 2007 were thought to have spawned based on several criteria. However, about 135 thousand smolts were produced from the 2006 brood of 3509 spawners counted through the fence (DFO, unpublished data; 38.5 smolts/spawner) suggesting the prespawning mortality was probably much lower, perhaps in the 20-30% range. This suggests that handling effects on tagged fish may have played a role in the level of pre-spawn mortality that we observed in study fish in both years. Because we can not rule out this possibility, interpretation of our results should be made with care.

Our efforts to relate longevity after 1 November, a rough surrogate for survival to the expected time of spawning, with lake entry were restricted to the 2007 data. Although limited by sample size, a non-linear relationship was detected between lake entry timing and survival, which suggested that early and late fish fared poorly relative to an intermediate arrival date. Historically, Cultus Lake sockeye have entered the lake as early as mid to late September (Schubert et al. 2002). Thus, the fish that were tagged in August and early September of 2007 are among those that have migrated upstream abnormally early, and the more optimal intermediate entry dates appeared consistent with arrival times corresponding to the normal dates of arrival under pre-1995 conditions.

Higher rates of pre-spawn mortality have previously been associated with early arrival even prior to the abnormal river entry timing phenomenon (Gilhousen 1990), and this has remained the case in more recent years (English et al. 2005). Sockeye that arrive early will be exposed to higher temperatures in the Fraser River during their migration to Cultus Lake (Patterson et al. 2007). Although the Vedder River is generally cooler, their final ascent to Cultus Lake is through the particularly warm Sweltzer Creek, which usually exceeds 20 °C in late summer. Mortality in fish that arrive at the lake early may be attributable to several potential mechanisms. Under warmer conditions, fish may accrue physiological stress, and consume limited energy reserves at an accelerated rate or limit the aerobic scope for performance (Cooke et al. 2004; Hinch et al. 2006; Farrell et al. 2008). This stress is likely compounded by the impacts of handling and tagging at the fence prior to entry to the cooler lake waters.

While similar mechanisms may have caused pre-spawning mortality in fish that arrived later in the season, relatively little is known of their history prior to lake entry. Nevertheless, histological studies have shown that fish arriving at the lake later in the season are often suffering from more severe *Parvicapsula* infections (Bradford et al. 2009). Within the captive broodstock program, those fish that were collected from the fence after October 15 were much less likely to survive to maturity than earlier migrants, probably as a result of *Parvicapsula* infections. Prolonged exposure to warmer temperatures in the Fraser River if they held there prior to moving into Cultus Lake would allow for development of the disease. Indeed, our observations of fish surfacing just prior to death may be an indication of severe gill tissue hyperplasia related to *Parvicapsula* infection (Bradford et al. 2009). Similarly, the additional stress induced by handling during tagging likely contributed to increased mortality compared to the general population.

In summary, we have been able to provide a detailed history of the depth and thermal behaviour of adult sockeye in Cultus Lake. This has revealed that fish largely remain below the thermocline where they are exposed to relatively cool temperatures for much of the time leading up to spawning. Nevertheless, in both years we observed substantial pre-spawning mortality in tagged fish. While we cannot discount the effects of tagging on fish survival, the observations of surfacing behaviour among many of the tagged sockeye supports the possibility of severe gill infection related to *Parvicapsula*, and may warrant further research into understanding how the surfacing behaviour relates to pre-spawning mortality. Although efforts to identify potential spawning locations were made, we were limited by small sample sizes as a result of high rates of mortality. Future studies in this area should consider alternate methods of locating spawning grounds or at a minimum, account for potentially high rates of mortality if tagging studies are used.

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Table 1. Summary of the dates on which 2006 fish were tagged, first detected in the lake, and when they died. Days in the lake are calculated as the difference between death and first lake detection. For fish 134 the U indicates that the sex was undetermined.

Fish ID	Sex	Tagging date, approx. time	First lake detection (date, time)	Death (date, time)	Days in Lake
131	F	03-Oct-06, 09:00	04-Oct-06, 10:30	20-Oct-06, 21:30	17.5
132	F	03-Oct-06, 09:00	04-Oct-06, 10:30	01-Nov-06, 06:45	27.8
133	F	03-Oct-06, 09:00	04-Oct-06, 11:30	23-Oct-06, 22:00	20.4
134	U	03-Oct-06, 09:00	04-Oct-06, 14:30	30-Oct-06, 11:15	24.9
135	F	03-Oct-06, 09:00	04-Oct-06, 10:30	08-Nov-06, 01:45	34.6
136	F	10-Oct-06, 09:00	10-Oct-06, 20:15	21-Oct-06, 20:45	11.5
137	M	10-Oct-06, 09:00	10-Oct-06, 18:00	28-Nov-06, 03:00	47.4
138	M	10-Oct-06, 09:00	10-Oct-06, 19:30	07-Nov-06, 09:00	26.6
139	M	10-Oct-06, 09:00	10-Oct-06, 17:00	28-Oct-06, 21:45	18.2
140	F	10-Oct-06, 09:00	10-Oct-06, 18:00	13-Oct-06, 18:00	3.0
141	F	10-Oct-06, 09:00	10-Oct-06, 18:15	03-Nov-06, 07:00	22.5
142	F	17-Oct-06, 09:00	17-Oct-06, 15:30	08-Nov-06, 01:00	20.4
143	F	17-Oct-06, 09:00	19-Oct-06, 17:45	23-Oct-06, 01:15	2.3
144	F	02-Nov-06, 09:00	N/A	N/A	N/A
145	F	02-Nov-06, 09:00	02-Nov-06, 17:15	10-Nov-06, 21:00	8.2

Table 2. Summary of the dates on which 2007 fish were tagged, first detected in the lake, and when they died. Days in the lake are calculated as the difference between death and first lake detection.

Fish ID	Sex	Tagging date, approx. time	First lake detection (date, time)	Death (date, time)	Days in Lake
147	F	21-Aug-07, 09:00	21-Aug-07, 09:45	05-Nov-07, 10:45	76.0
148	F	24-Aug-07, 09:00	24-Aug-07, 09:45	17-Oct-07, 15:45	55.3
149	F	21-Aug-07, 09:00	21-Aug-07, 09:00	22-Nov-07, 07:15	92.9
150	M	24-Aug-07, 09:00	24-Aug-07, 11:15	08-Nov-07, 20:00	77.4
151	F	28-Aug-07, 09:00	28-Aug-07, 10:45	22-Nov-07, 05:15	85.8
152	F	06-Sept-07, 09:00	06-Sept-07, 10:15	07-Nov-07, 10:15	62.0
153	M	06-Sept-07, 09:00	06-Sept-07, 10:30	14-Nov-07, 14:30	70.2
154	F	13-Sept-07, 09:00	13-Sept-07, 09:00	02-Dec-07, 17:00	81.3
155	F	13-Sept-07, 09:00	13-Sept-07, 11:00	02-Dec-07, 04:15	79.7
157	M	20-Sept-07, 09:00	20-Sept-07, 09:30	02-Dec-07, 05:30	72.8
158	F	20-Sept-07, 09:00	20-Sept-07, 09:30	25-Nov-07, 04:15	65.8
159	F	20-Sept-07, 09:00	20-Sept-07, 10:15	02-Dec-07, 13:45	74.1
160	F	27-Sept-07, 09:00	27-Sept-07, 09:30	28-Nov-07, 08:00	61.9
161	F	28-Sept-07, 09:00	28-Sept-07, 10:00	23-Nov-07, 01:30	55.6
162	F	04-Oct-07, 09:00	04-Oct-07, 10:15	17-Nov-07, 21:45	45.5
163	F	04-Oct-07, 09:00	04-Oct-07, 09:45	13-Nov-07, 02:30	39.7
164	F	04-Oct-07, 09:00	04-Oct-07, 09:30	19-Oct-07, 17:45	16.3
165	F	05-Oct-07, 09:00	04-Oct-07, 09:15	04-Dec-07, 23:30	62.6
166	F	18-Oct-07, 09:00	18-Oct-07, 10:00	05-Nov-07, 23:15	19.6
167	M	26-Oct-07, 09:00	26-Oct-07, 11:00	08-Nov-07, 11:30	13.5

Table 3. Summary of the mean depths and estimated mean temperatures for fish tagged in 2006, over all data, and separated by day and night.

Fish ID	Mean depth (m)			Mean temperature (^oC)		
	Total	Day	Night	Total	Day	Night
131	20.41	20.38	20.45	8.00	7.85	8.14
132	23.26	23.68	22.89	6.77	6.71	6.83
133	17.15	18.69	15.56	8.72	8.02	9.44
134	14.86	15.79	14.01	9.49	9.06	9.89
135	18.68	19.67	17.72	7.69	7.42	7.96
136	17.17	17.07	17.26	8.64	8.60	8.67
137	17.14	17.82	16.59	7.44	7.29	7.55
138	19.49	19.60	19.38	7.22	7.13	7.31
139	18.90	19.05	18.77	7.24	7.25	7.23
140	11.36	13.16	9.70	10.64	9.57	11.63
141	16.19	15.95	16.41	7.96	7.85	8.05
142	13.69	12.99	14.28	8.34	8.59	8.13
143	13.01	12.94	13.08	9.63	9.75	9.52
145	3.67	4.87	2.52	10.55	10.40	10.69
131	20.41	20.38	20.45	8.00	7.85	8.14

Table 4. Summary of the mean depths and estimated mean temperatures for fish tagged in 2007, over all data, and separated by day and night.

Fish ID	Mean Depth (m)			Mean Temperature (^{o}C)		
	Total	Day	Night	Total	Day	Night
147	20.05	20.90	19.04	7.33	7.20	7.47
148	21.81	22.38	21.08	6.62	6.59	6.65
149	20.87	22.10	19.46	7.05	6.92	7.20
150	21.75	23.91	19.20	7.02	6.82	7.25
151	19.91	20.74	19.07	7.24	7.08	7.41
152	21.01	21.74	20.10	7.17	7.12	7.24
153	20.64	21.26	19.95	7.04	6.94	7.14
154	17.37	18.76	15.68	7.79	7.52	8.13
155	20.12	19.82	20.41	7.17	7.13	7.20
157	20.56	21.17	19.96	7.09	6.98	7.20
158	15.98	17.02	14.98	7.79	7.69	7.89
159	11.80	13.60	10.00	8.03	7.77	8.29
160	18.48	19.06	17.90	7.62	7.57	7.67
161	18.26	19.48	17.20	7.53	7.34	7.70
162	14.90	16.06	13.72	8.06	7.87	8.25
163	17.03	17.43	16.64	7.87	7.86	7.89
164	22.22	22.82	21.58	7.73	7.58	7.89
165	19.83	22.08	17.76	7.31	7.08	7.52
166	15.15	15.03	15.25	8.99	9.05	8.95
167	15.42	15.60	15.23	8.62	8.54	8.71

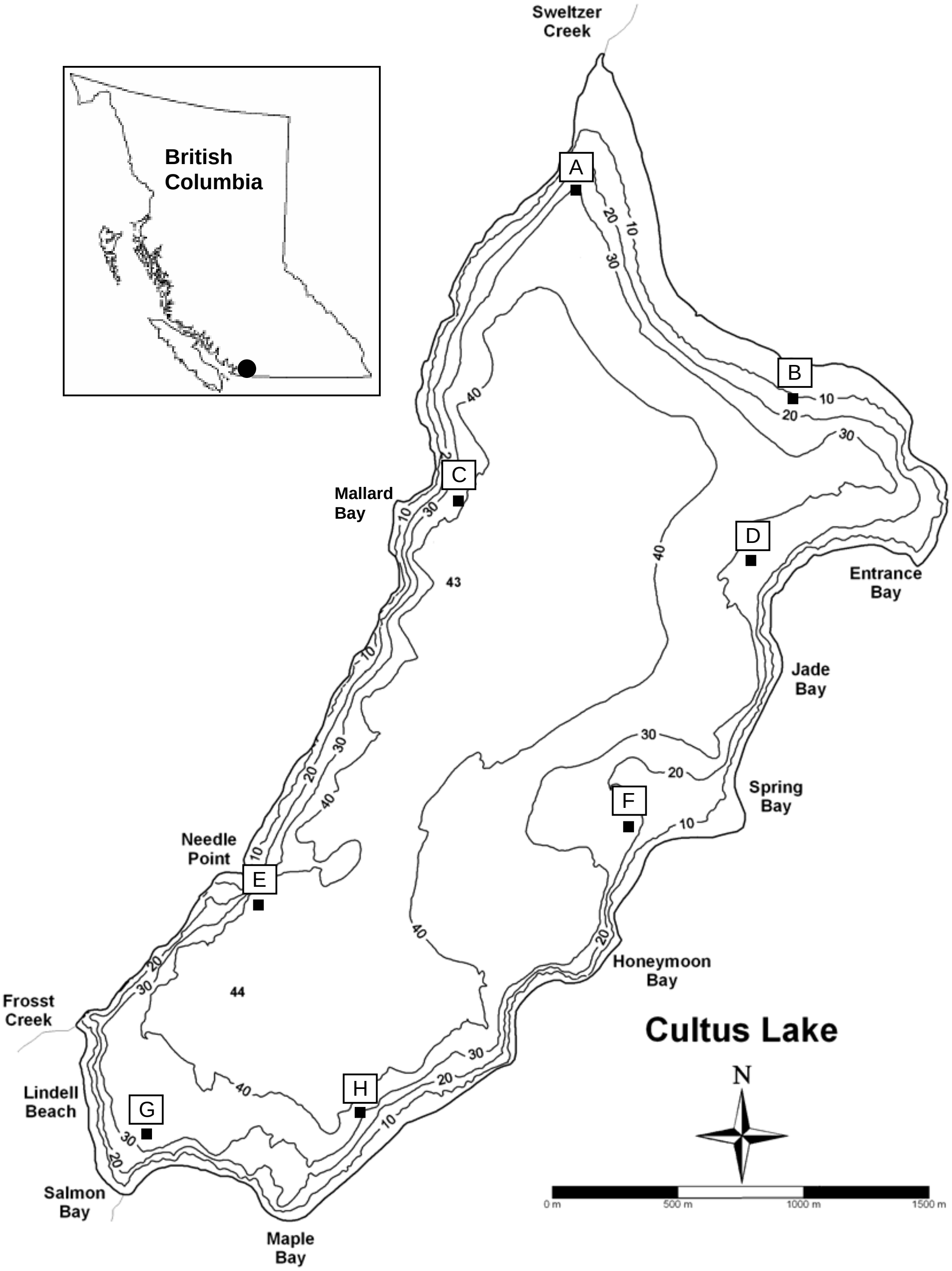

Figure 1. Map of Cultus Lake showing the locations of hydroacoustic receivers A through H. Receivers had an effective detection radius ranging from 1280 m to 2110 m.

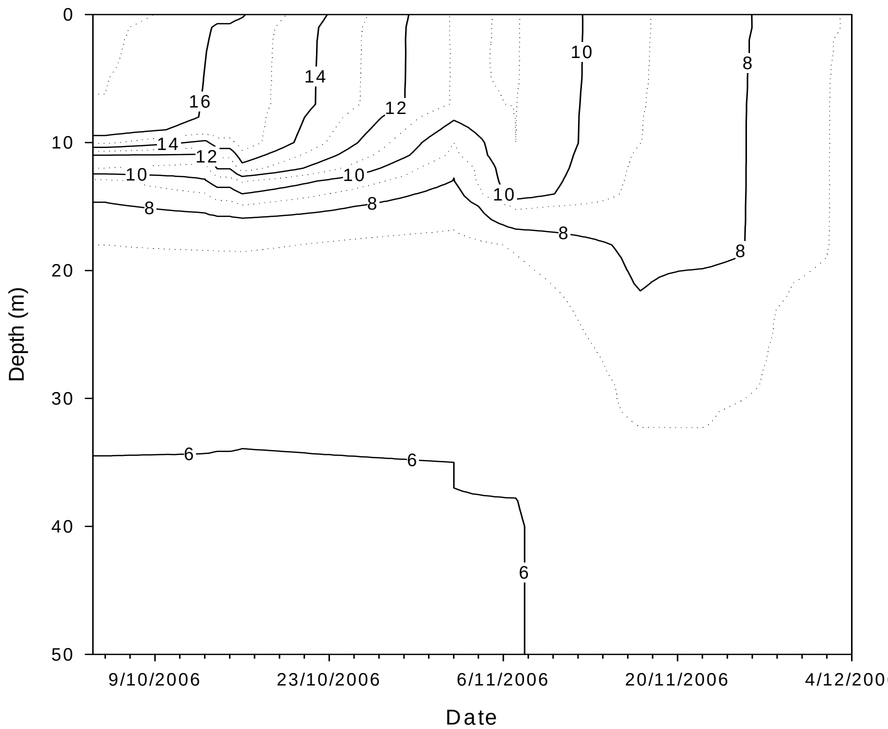

Figure 2. Cultus Lake temperatures by depth over the period 4 October to 4 December, 2006.

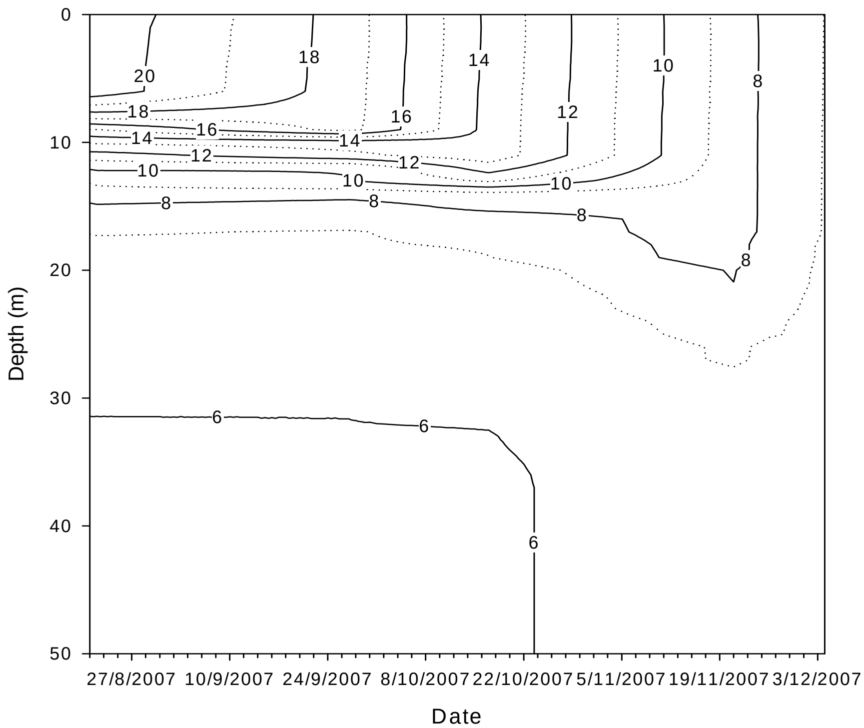

Figure 3. Cultus Lake temperatures by depth over the period 21 August to 4 December, 2007.

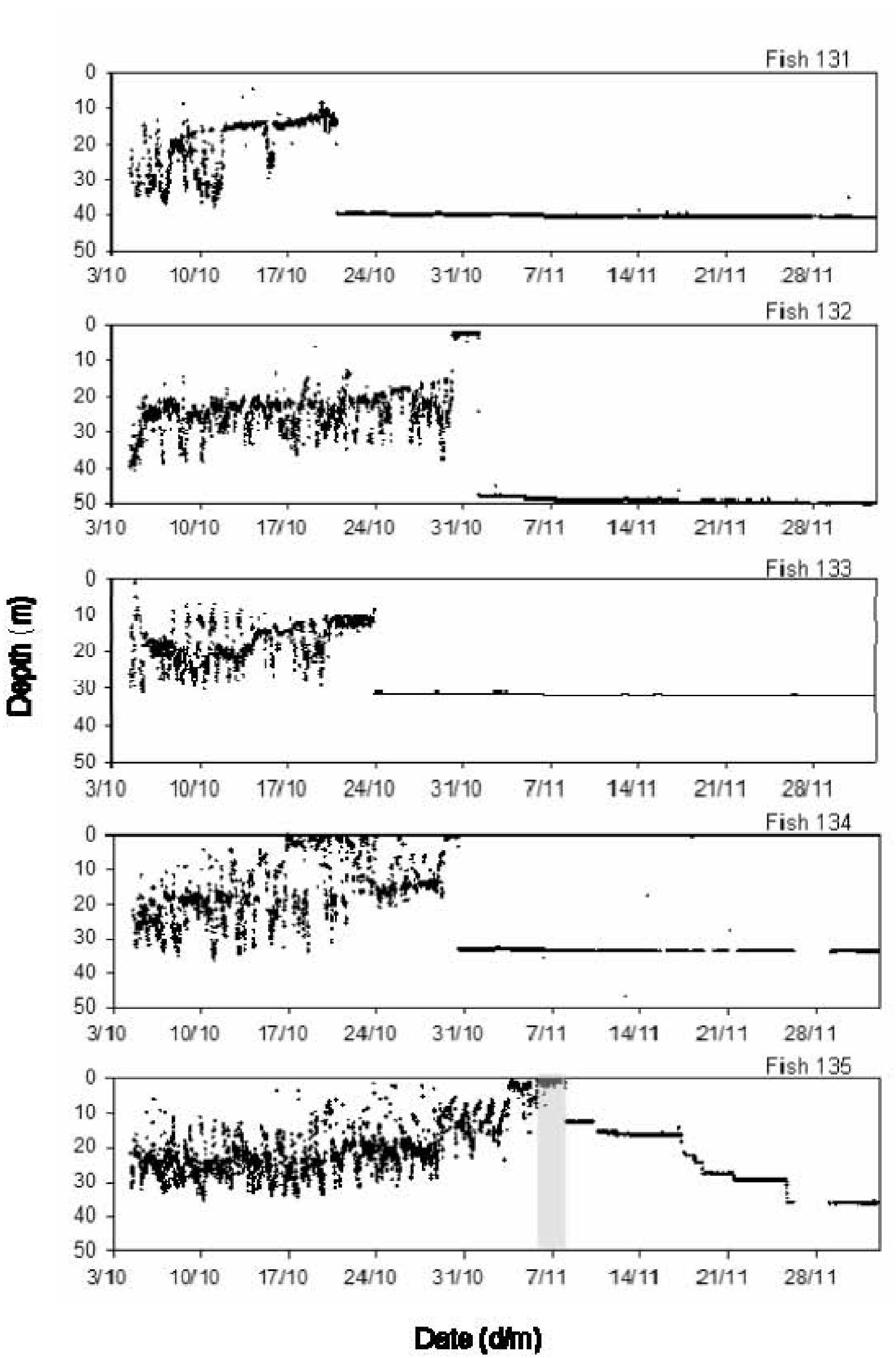

Figure 4. Depth recordings for individual fish plotted over the 2006 study period. The timings of potential spawning events are indicated by grey boxes for fish that were determined to have spawned.

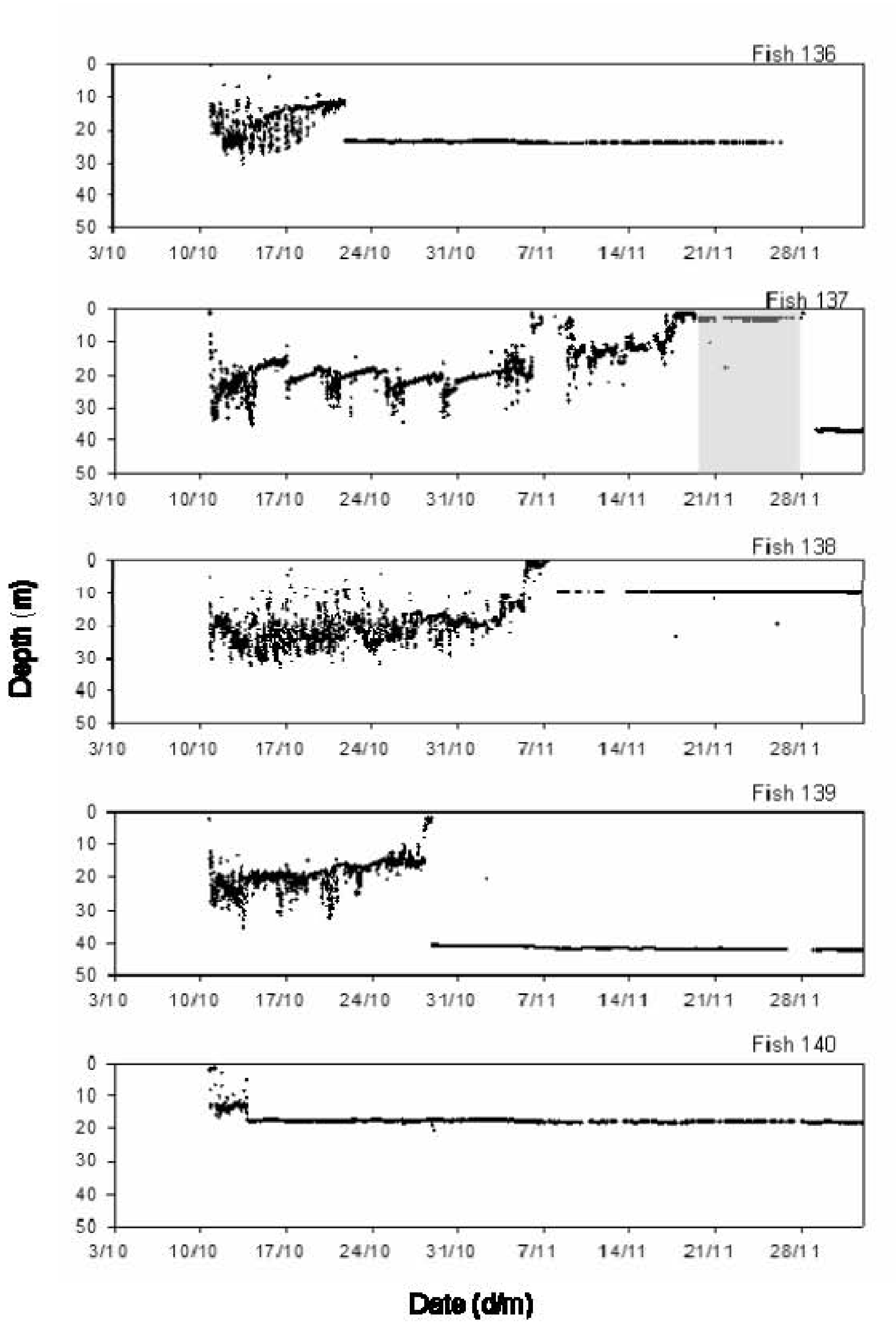

Figure 4 cont.

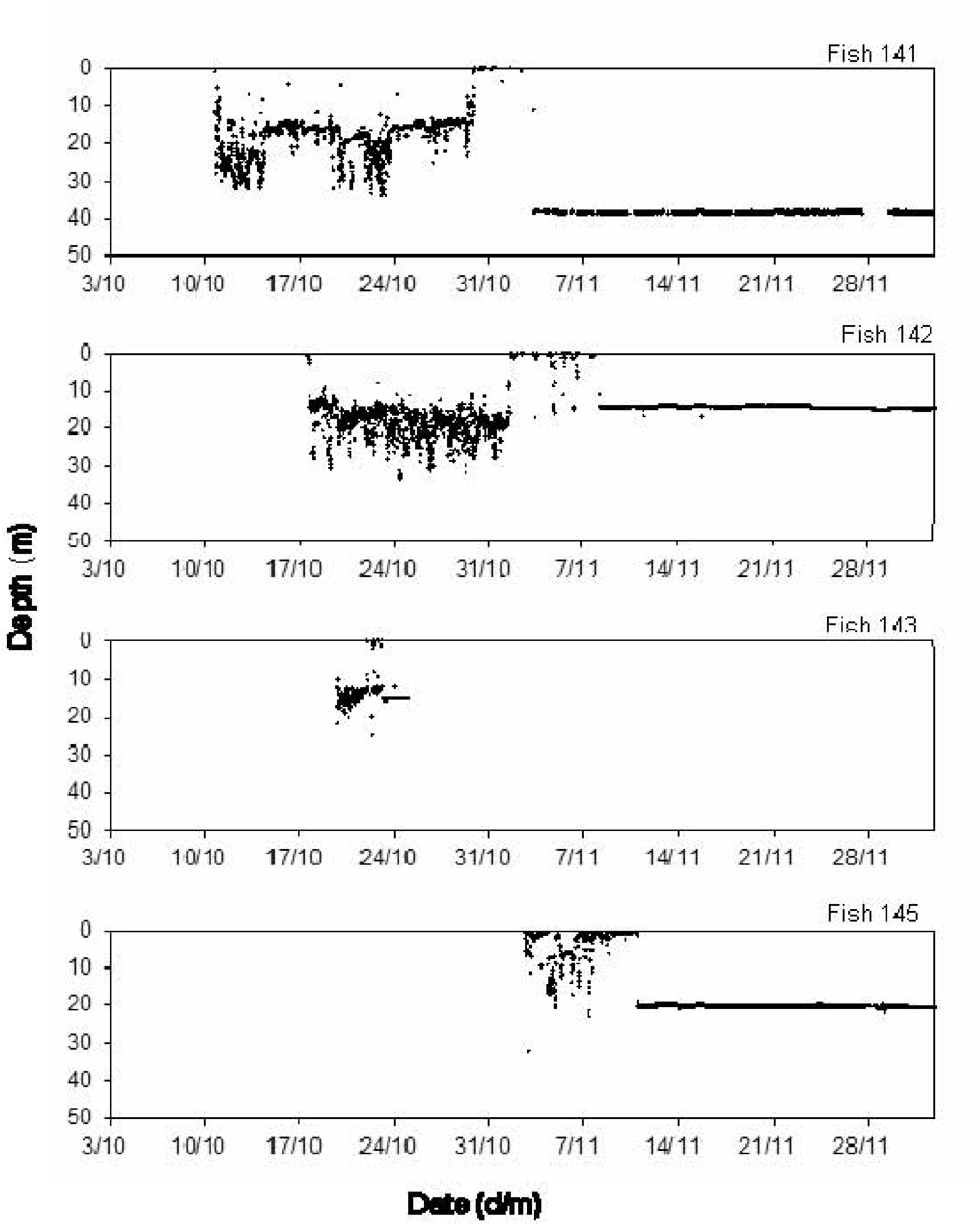

Figure 4 cont.

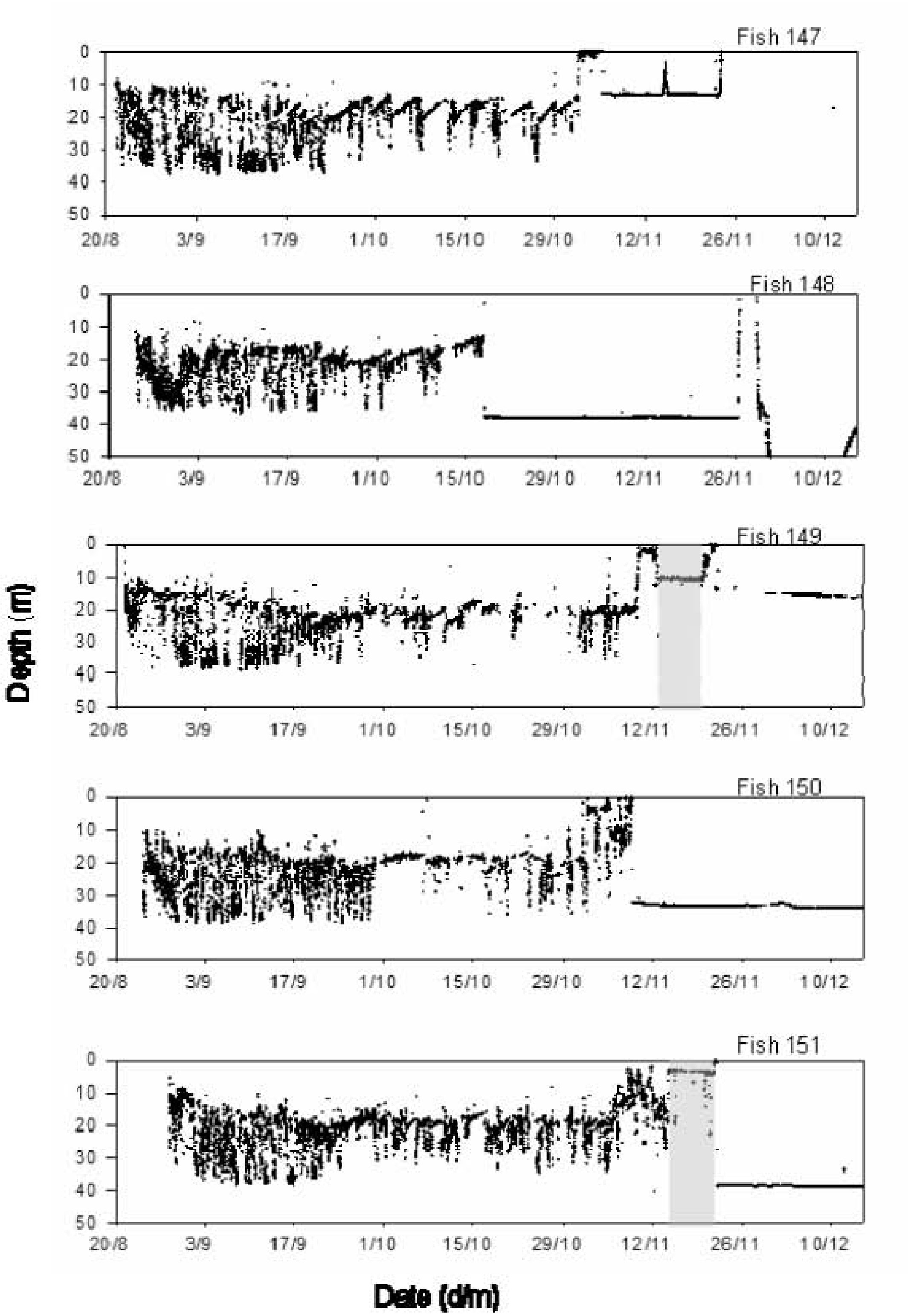

Figure 5. Depth recordings for individual fish plotted over the 2007 study period. The timings of potential spawning events are indicated by grey boxes for fish that were determined to have spawned.

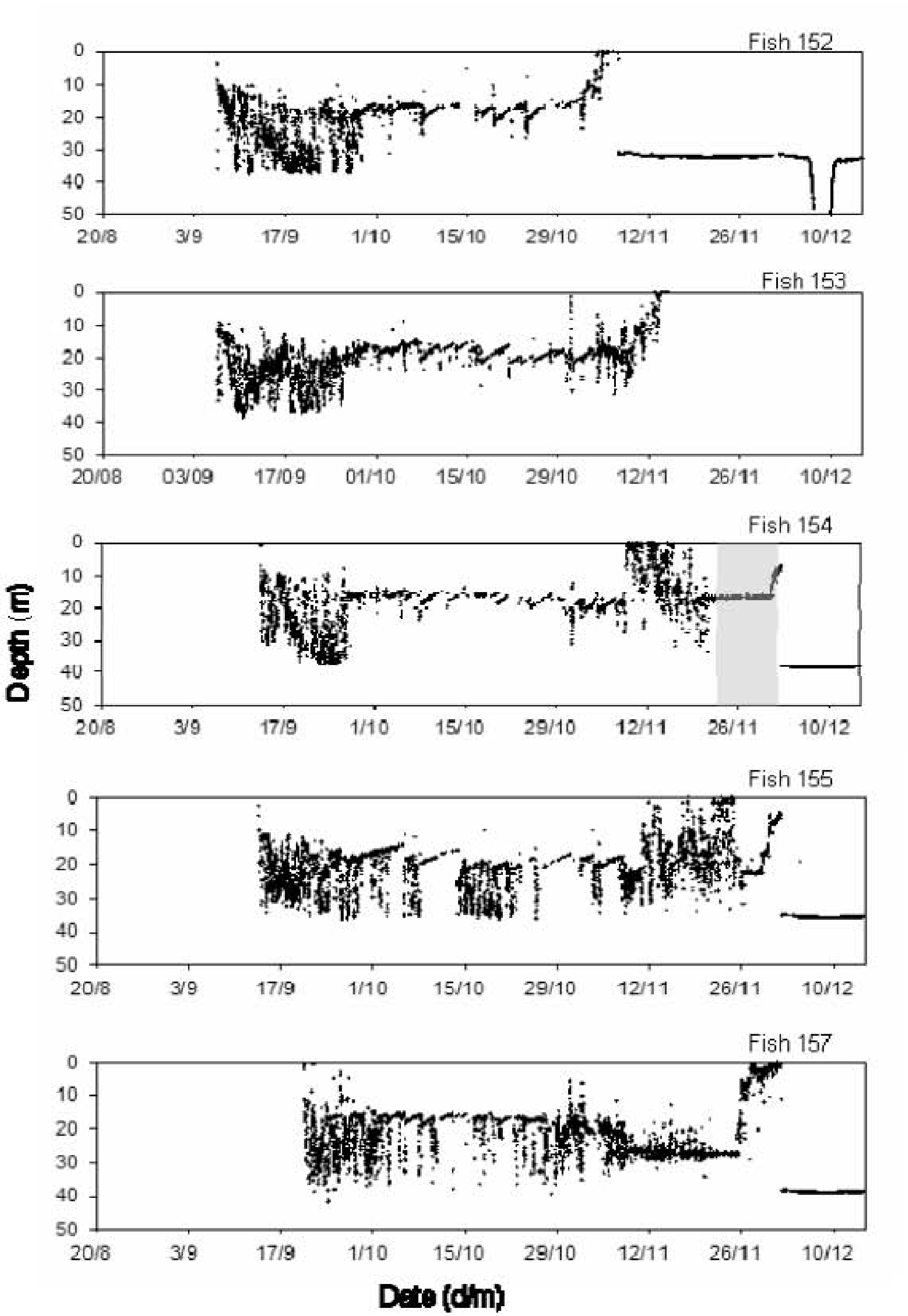

Figure 5 cont.

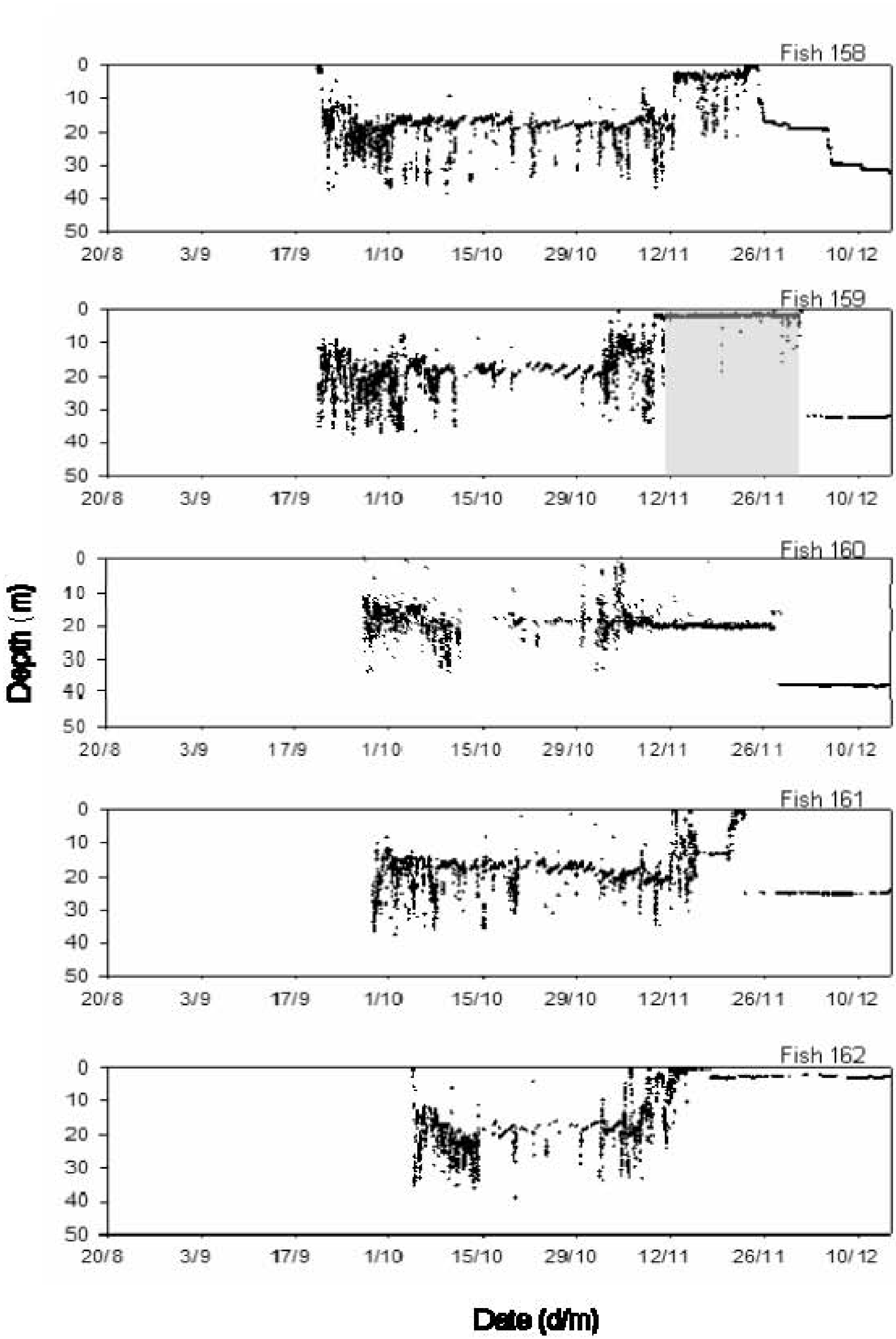

Figure 5 cont.

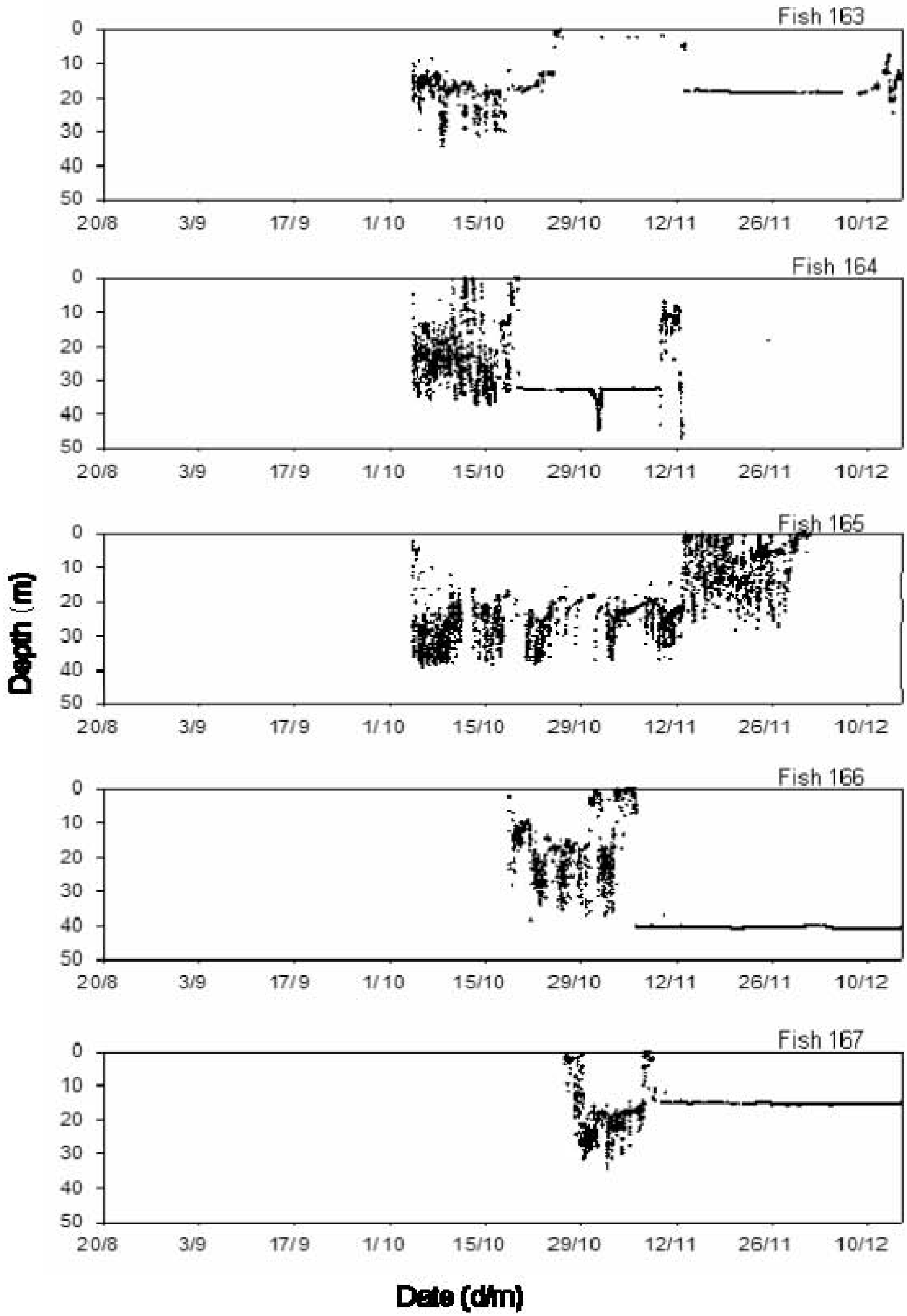

Figure 5 cont.

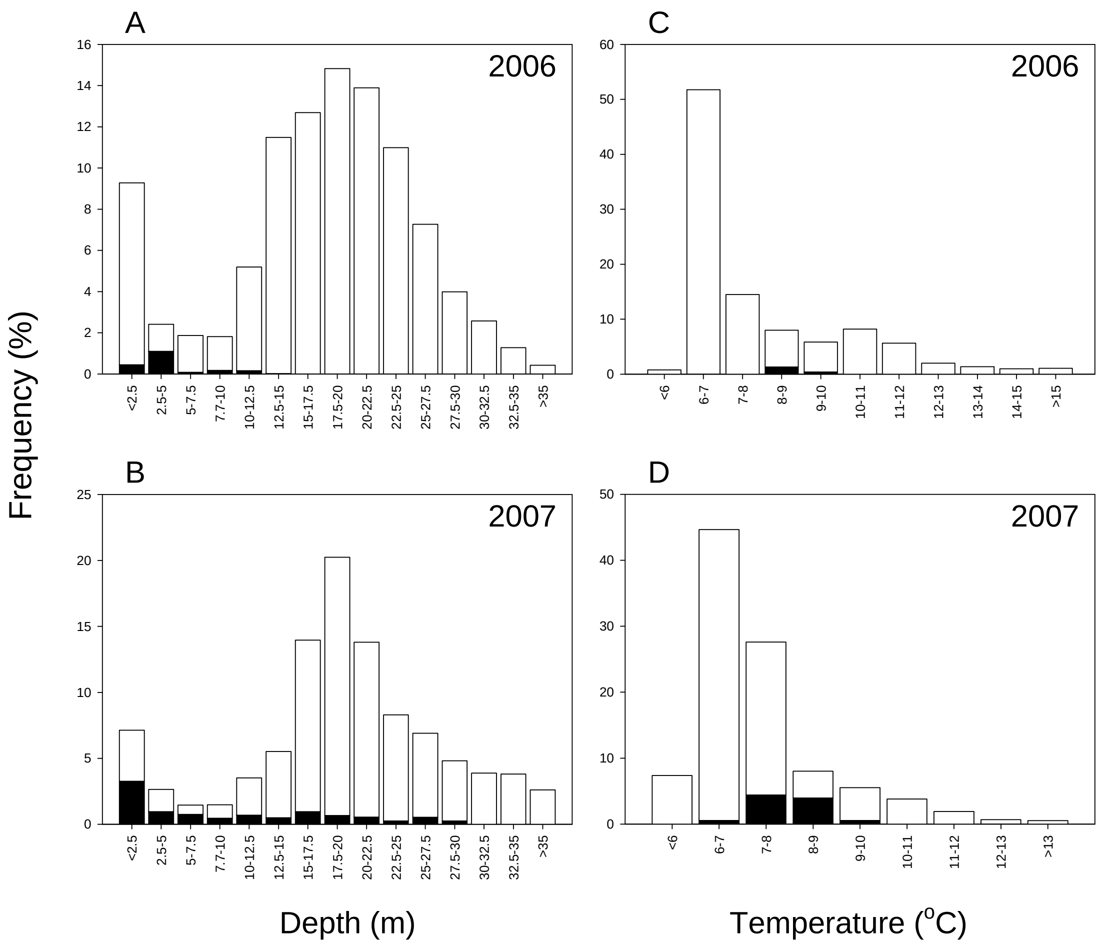

Figure 6. Frequency distributions of depths and temperatures that tagged sockeye salmon were recorded at while in Cultus Lake in 2006 and 2007. The white part of the bar represents the frequency at which depths or temperatures were recorded before 15 November, or when the lake was stratified. The black part of the bar represents the frequency at which depths or temperatures were recorded after 15 November, or approximately when the lake mixed.

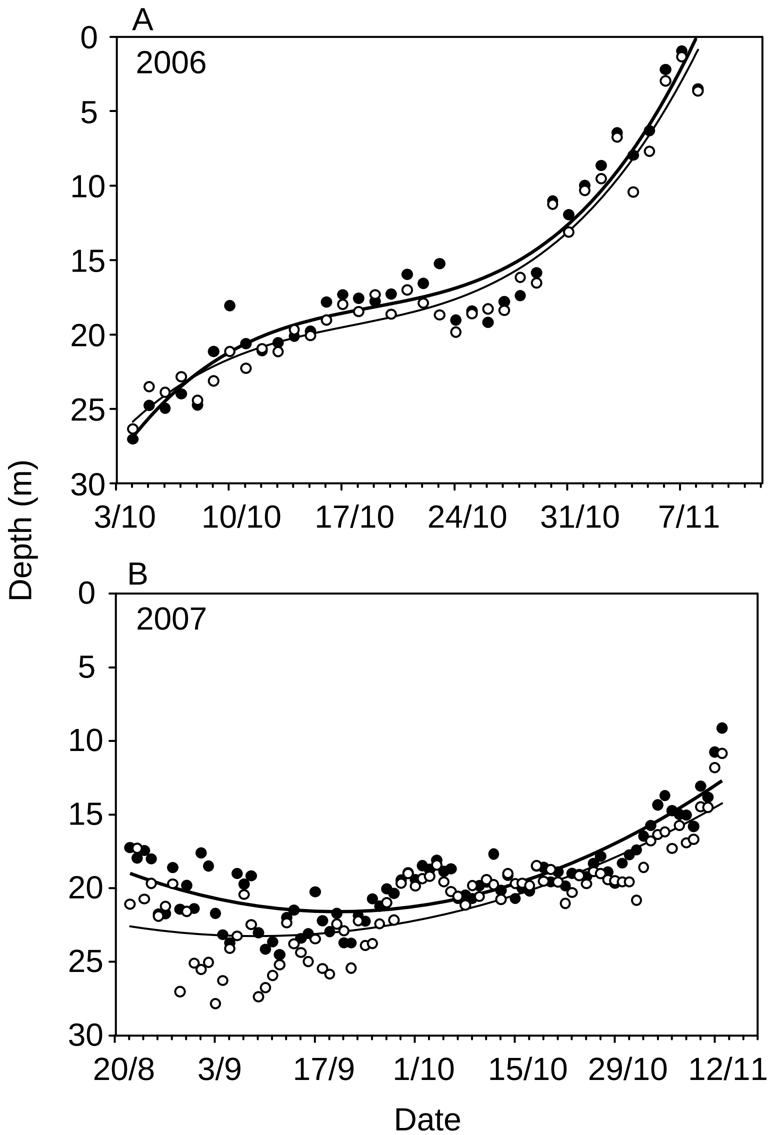

Figure 7. Non-linear relationships between depth and study date (2006: day: R^2 = 0.95; night: R^2 = 0.94; 2007: day: R^2 = 0.64; night: R^2 = 0.70; all P < 0.001). Depth in both years was calculated as a mean across all tagged fish that were present in the lake for a given date. Open circles represent mean day depths, closed circles represent mean night depths. The bolded regression line is fit to the night depth data.

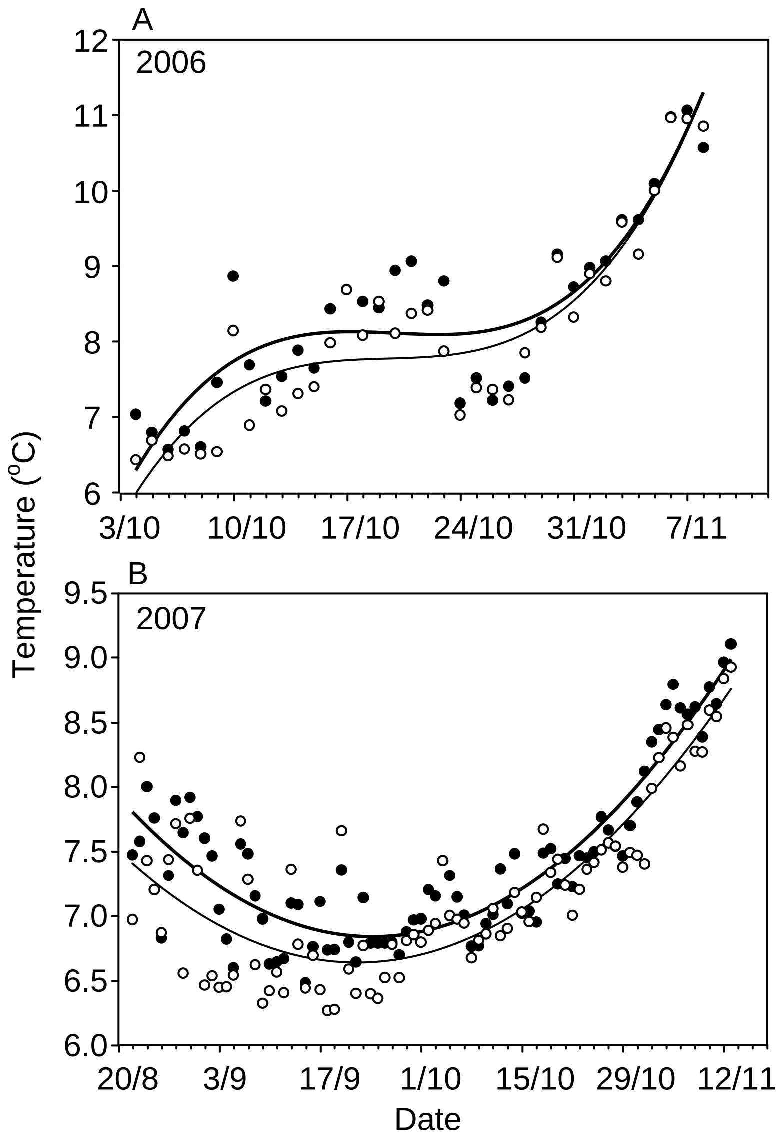

Figure 8. Non-linear relationships between water temperature and study date (2006: day: *R2* = 0.85; night: *R2* = 0.77; 2007: day: *R2* = 0.75; night: *R2* = 0.82; all *P* < 0.001). Temperature in both years was calculated as a mean across all tagged fish that were present in the lake for a given date. Open circles represent mean day temperatures, closed circles represent mean night temperatures. The bolded regression line is fit to the night temperature data.

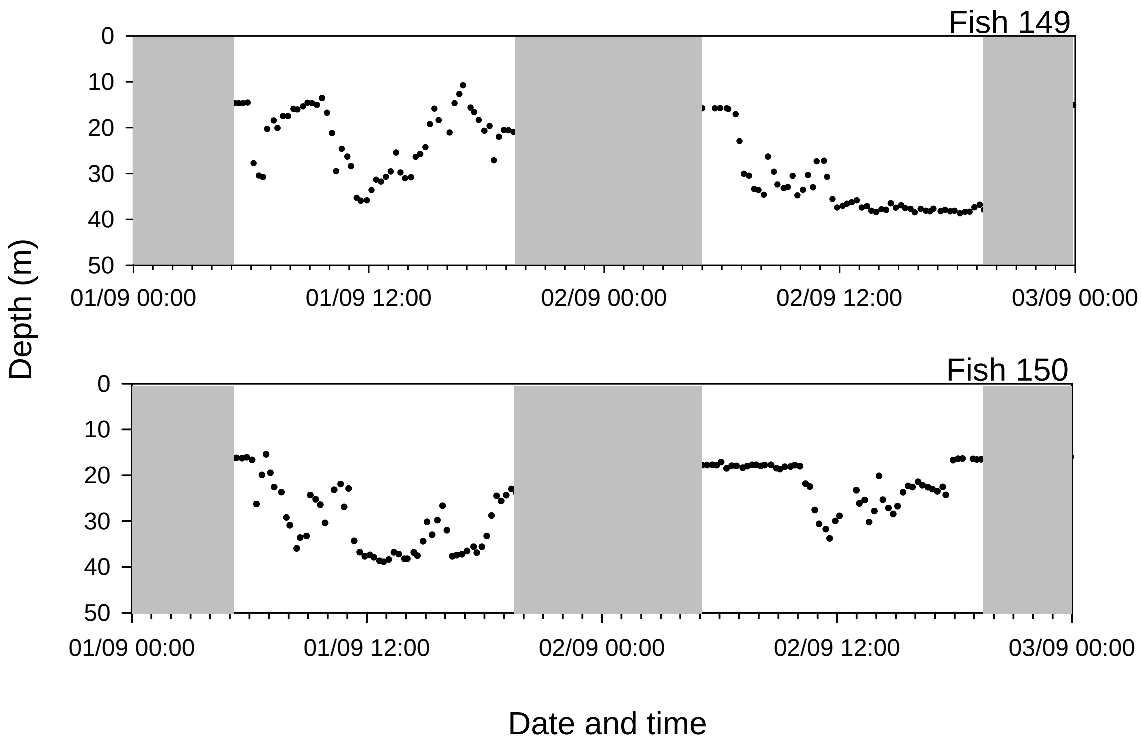

Figure 9. Detail of diel variation in depth for from two fish that entered Cultus Lake early in the 2007 study period. Time periods corresponding to night based on civil twilight are indicated by grey boxes.

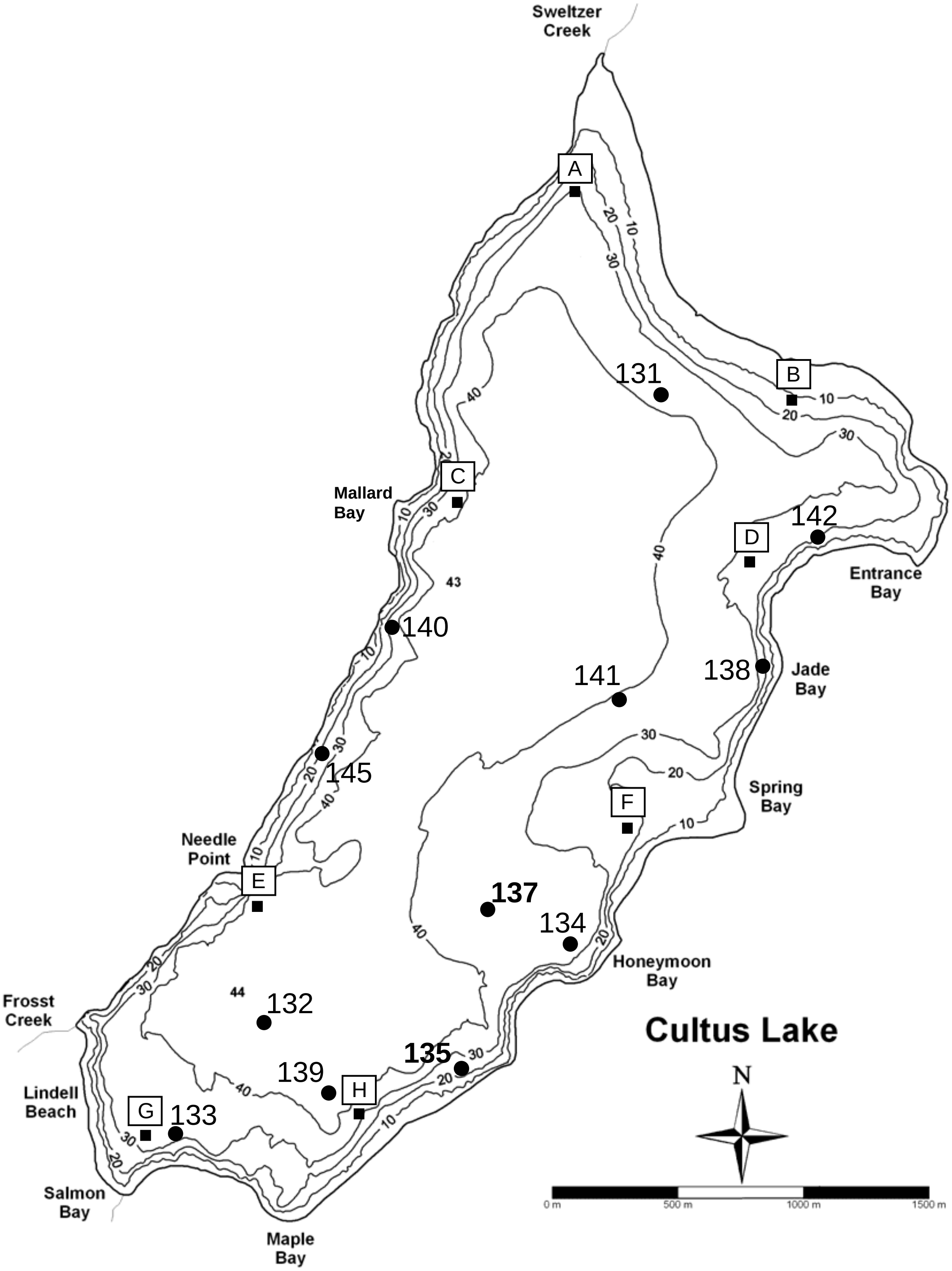

Figure 10. Map of Cultus Lake showing the locations of 2006 tags from the survey conducted on 1 February, 2007. Potential spawners (fish #135 and #137) are shown in bold. Fish #143 is not shown as it had disappeared from the lake on 23 October. Letters A-H designate the receiver locations.

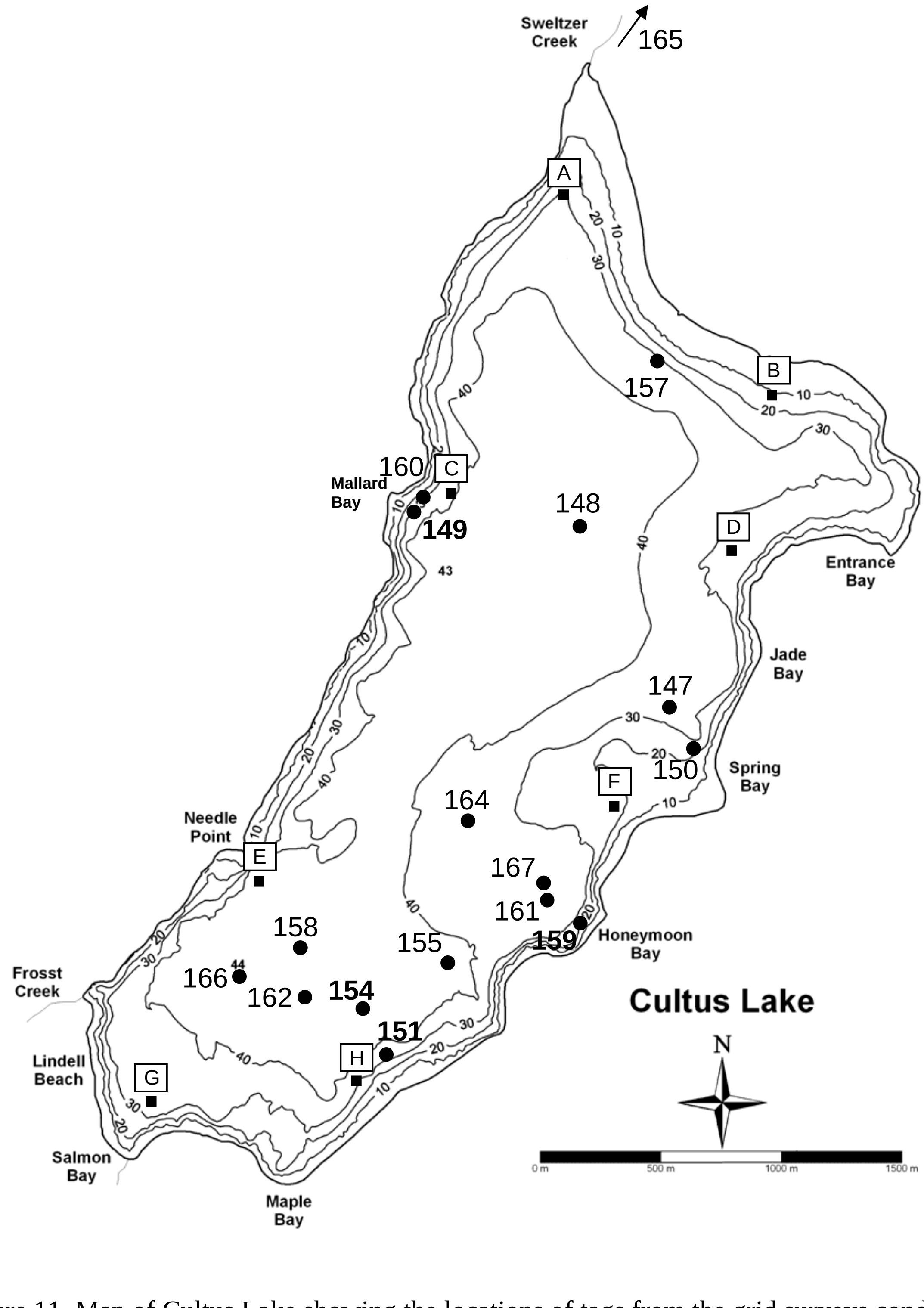

Figure 11. Map of Cultus Lake showing the locations of tags from the grid surveys conducted at the end of the 2007 study period. Potential spawners (fish 149, 151, 154, 159) are shown in bold. Fish 165 was found at the confluence of Sweltzer Creek and the Vedder River. Letters A-H designate the receiver locations.

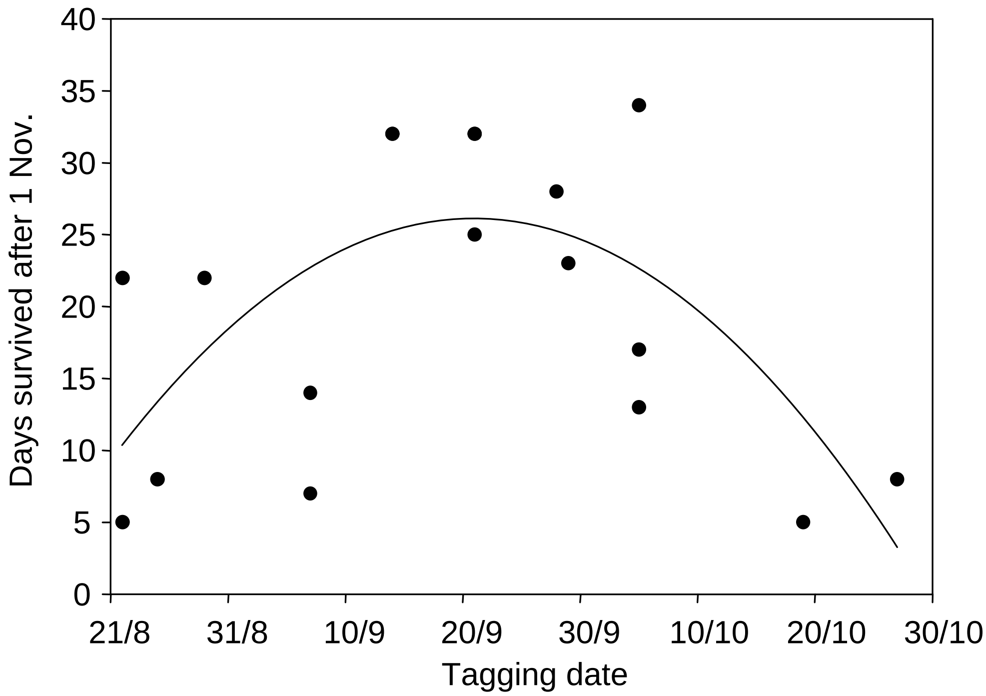

Figure 12. Non-linear relationship between lake entry date for 2007 fish and the number of days a fish survived after 1 November (*R2* = 0.445, *P* = 0.012). The survival index was used as a surrogate for survival to spawning due to the high rate of pre-spawning mortality that we observed (80%).