Predicting lake trout spawning areas in Yellowstone Lake as a part of the native Yellowstone cutthroat trout preservation program in Yellowstone National Park

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EXECUTIVE SUMMARY

Decreases in biodiversity are occurring worldwide because of the spread of invasive species, and by some standards, this spread is the largest threat to worldwide biodiversity. This study is an effort to examine one potential pathway of expansion for one invasive species, lake trout *Salvelinus namaycush,* in one habitat, Yellowstone Lake, Wyoming.

Lake trout were first verified as being present in Yellowstone Lake in 1994. This caused serious concern because lake trout are known to be a voracious piscivore and native Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* were expected to be the main prey item for larger lake trout. The National Park Service initiated a lake trout suppression program in hopes of reducing lake trout impacts to the cutthroat trout population. Currently most lake trout spawning in Yellowstone Lake is believed to occur in the West Thumb portion of the lake. As the population increases, new spawning areas will probably be pioneered, expanding recruitment to the population.

We surveyed three suspected spawning areas in Yellowstone Lake to determine the presence of suitable spawning substrate. Small patches of suitable substrate were found at two of the areas, and no suitable substrate was found at the third area. Additional habitat features of water depth, fetch length, aspect, slope, and distances to refuge depths of 20-30m, to the nearest thermal vents that may affect water quality, and to shore were summarized for each patch.

Using a high resolution bathymetry data layer and ArcGIS capabilities, a multilayer habitat suitability index model was constructed. Published values for water depth, fetch length, slope, and location within or out of the wave energy zones for particle erosion and deposition were used in the hypothesized model. Values for distance to depths greater than 30m were also included. The model classified over 88% of the lake as unsuitable and under 6% as having excellent potential to provide suitable spawning habitat for lake trout. Further refinement, including sensitivity analysis and sophistication of processes for data recombination, will increase the predictive ability of the model.

INTRODUCTION

Invasive species constitute a huge threat to biodiversity world-wide. Their spread into new areas is precipitating a global ecological and conservation crisis as invaders alter terrestrial and aquatic communities (Cambray 2003; Gurevitch and Padilla 2004; Normile 2004). Consequences range from declines in native species, elimination of native fauna, and reduction of species richness to disruption of ecological processes, which can lead to cascading ecosystem effects. Invasions by non-native species are a leading cause of species extinctions (Gurevitch and Padilla 2004; Quist and Hubert 2004) and pose a significant problem for native species conservation in the western United States (Quist and Hubert 2004). All of these effects can lead to wide-ranging ecological and economic impacts (Simberloff et al. 2005).

Invasive species are successful for a variety of reasons. Some possible mechanisms include lack of a defense or buffer system within the native ecosystem against the invasive species. Having no previous contact with the invasive species, there was no need to evolve such strategies to prevent its expansion. Areas where local fauna or flora are already stressed or have been disturbed, for example by habitat alterations, and have not had time to adapt or recover often present prime areas for invasive species to gain a foothold.

Once a foothold has been established, population expansion follows. Increase in population biomass is a function of recruitment, growth, and mortality. Population size increases by increased recruitment and growth, decreased mortality, or a combination of the three. Range expansion is dependent on the population size and dispersal mechanisms. Dispersal can occur fairly uniformly to fill (or dominate) available habitat in areas with fairly uniform habitat. In areas with patchy habitat, colonization of new habitat patches may require: (1) a population density high enough at an occupied patch to trigger dispersal or (2) a movement pattern or corridor that allows the invader to disperse from the occupied patch to an unoccupied patch. An obvious requirement of successful dispersal is that the dispersing individuals be able to find the new patches.

Without interference, or control efforts, an invasive species may expand until it fully occupies available habitat to either the exclusion of native fauna or until some balanced (albeit reduced) existence is found between the native fauna and the invader (Baxter et al. 2004). In either case, damage to the ecosystem occurs and the full dimensions of the damage may not be recognized. Often, in efforts to reverse or minimize ecosystem damage, control efforts to reduce or eliminate the invader population are implemented.

Control or removal efforts of invasive species are often ineffective. Directed at decreasing population size by enhancing mortality rates of individuals, control efforts require large amounts of manpower and funding, consuming valuable resources which are then not available for other important resource work. Common techniques used to control invasive fishes include chemical, biological, or mechanical methods (Wydoski and Wiley 1999).

Chemical methods involve introducing toxins into the environment which will kill the invasive fish species. This has been widely used in fisheries management for ‘reclaiming’ lakes in the past (i.e., removal of an undesired species and reintroduction of species considered desirable either for ecosystem restoration or sport-fish enhancement projects). Toxins are generally not specific to the target organism and often require detoxification with additional chemicals to contain impacts. A multitude of examples exist where detoxification failed, causing fatality to many unattended organisms. Except in rare circumstances (*e.g.*, sea lamprey *Petromyzon marinus* control in the Great Lakes region), large-scale applications of toxic chemicals to public waters is no longer politically, socially, or environmentally acceptable. Because large amounts of toxins would be required to impact invasive species in most aquatic systems, this is not a viable option for large systems.

Likewise, biological control has many associated risks. Biological control generally consists of identifying a natural predator or pathogen to the invasive species from its native environment and introducing it into the ecosystem of concern. It is literally impossible to evaluate the effects of such introductions and past attempts have often resulted in unintended cascading ecosystem impacts. Thus, this option is also difficult to apply to large systems.

This suggests that mechanical control offers the best solution to controlling an invasive fish species. Generally, some sort of capture effort (*e.g.*, netting or electrofishing) is used and resultant catches are removed from the system. However, this method tends to be very labor intensive and often ineffective (Wydoski and Wiley 1999).

Another potential problem with traditional control methods concerns the response curve of the ecosystem to removal efforts. Scheffer et al. (2001)

reviewed several examples of systems where the response curve exhibited two unique stable states, separated by an unstable equilibrium, and was essentially folded back on itself (Figure 1-1). Basically, gradual increase in a given stressor to the ecosystem may have little to no effect until some threshold value is reached. After the threshold is passed a ‘catastrophic’ transition occurs which plummets the ecosystem from its current state to an alternate stable state. In order to recover the original stable state, drastic measures may need to be taken to reduce the stressor well beyond the initial threshold value which caused the original shift. This switching between the two states is referred to as hysteresis (Scheffer et al. 2001).

A well-studied example of this type of ecosystem behavior hypothesized by Scheffer et al. (2001) concerns water clarity and vegetation observed in shallow lakes subject to human-induced eutrophication. Water clarity appears to be hardly effected by increased nutrient loads until some critical threshold is passed. Once passed, an increase in algal blooms is seen, quickly shifting lake water from clear to turbid. This leads to loss of macrophytes and associated invertebrate diversity in the productive littoral zone of the lake. Reduction of nutrient loads to below the critical threshold will not restore the vegetated, clear water state of the lake. In fact, nutrient loading must be substantially reduced below the critical threshold in order to reduce algal growth, clear the water, and allow for macrophyte recovery (Scheffer et al. 2001).

This phenomenon could potentially occur with removal efforts of invasive fish species. If a hysteresis effect exists, levels of the invasive species which led to a catastrophic change in the state of ecosystem need to be greatly reduced, well past the observed threshold level which produced the original shift, in order to allow for recovery to the original state. If this were the case, removal efforts could be allowing the invasive species to persist at a level that allows maximal population growth, creating an endlessly altered ecosystem.

In this situation, despite a large amount of effort directed toward removal or control of the invasive fish species and visible reductions in its population level, it is possible that recovery of the system may not be seen. Eventually, given the political nature of support for this type of effort, funding could be redirected and the recovery effort abandoned. Even if reductions are effective, adequate funding to keep the invader suppressed could be withdrawn, allowing the invading population to explode (Simberloff et al. 2005).

An alternative to the traditional approach of controlling an invasive species is to identify actual pathways of population expansion and focus attention on disrupting these pathways. For example, rather than expending sizeable amounts of limited resources (money, personnel time, and equipment) decreasing population size, which is typically very costly and often ineffective, efforts are focused on disrupting the pathway of expansion. Application of this approach requires knowledge of the distribution and availability of critical habitat patches, the level of saturation (i.e., density of the invasive species) within critical patches that leads to dispersal, movement corridors between patches that allow colonization of new patches, and the extent of colonization of new patches that allow increases in population size.

To demonstrate this approach, consider control of lake trout *Salvelinus namaycush* outside of its native range in the Intermountain West, specifically in Yellowstone Lake, Yellowstone National Park, Wyoming. Generally regarded as an economically important and highly desired sport fish species throughout much of North America, lake trout have been widely introduced into lakes outside their native range (Behnke 2002; Martin and Olver 1980; Scott and Crossman 1973). A highly efficient piscivore, they can quickly become the dominant predator, causing a variety of ecosystem disruptions (or shifts in state), including severe reductions in or extinction of native species when introduced to new areas.

Establishment of lake trout is believed to have led to declines of native cutthroat trout *Oncorhynchus clarki* populations in several western North American lakes including Bear Lake, Idaho-Utah (Ruzycki et al. 2001); Lake Tahoe, California-Nevada (Cordone and Frantz 1966); Heart Lake, Yellowstone National Park (Dean and Varley 1974); and Jackson Lake, Grand Teton National Park (Behnke 1992). Where nonnative lake trout and native cutthroat trout occur together, cutthroat trout populations have often declined, have exhibited slower growth and truncated size distributions, or have disappeared. The mechanisms of these impacts vary among waters, but include direct predation and competition for shared resources.

Further, several management agencies throughout the West continue to struggle with how to control the populations of lake trout (Martinez et al. *in review)*. For example, replacement of or competition with native bull trout *Salvelinus confluentus* in Priest Lake in northern Idaho and several lakes in western Montana, including Flathead Lake and lakes in western Glacier National Park, is of grave concern to fisheries managers (Deleray et al. 1999; Maiolie et al. 2005; Marnell 1986).

Direct impacts of lake trout populations are also of concern to many management agencies in the West (Martinez et al. *in review*). Even in less natural areas, such as Flaming Gorge and Blue Mesa reservoirs of Wyoming and Colorado, over-abundant lake trout cause ecosystem-level concerns (Johnson and Martinez 2000; Luecke et al. 1999; Yule and Luecke 1993). For example, reduction of kokanee *Oncorhynchus nerkii*, the main prey species for lake trout in many Colorado systems, could lead to the collapse of those populations and subsequent impacts to, in these cases, the highly desirable lake trout populations themselves (Crockett 2004; Johnson and Martinez 2000)

Invasive lake trout in Yellowstone Lake provide an opportunity to examine the idea of disrupting expansion pathways for several reasons. They are a relatively new invader and it appears the population is currently expanding (Koel et al. 2005; Munro et al. 2005). They are thought to show a high fidelity to natal spawning areas, thus spawning areas can represent critical habitat patches. Use of these areas can be considered as a pathway to population expansion which can be exploited in efforts to control lake trout. The apparent increase in size of the spawning population will undoubtedly lead to discovery and colonization of new spawning areas, giving an example of another pathway which could be exploited. The current strategy of mechanical removal is labor intensive, costly, and vulnerable to discontinuation based on political whims. Finally, although thousands of lake trout are being removed from Yellowstone Lake annually, the level of reduction will not be enough to allow recovery of the native Yellowstone cutthroat trout population to its prior stable state.

Exploration of these ideas involves verification that spawning areas do indeed represent critical habitat patches (i.e., suitable spawning areas are rare and relatively small within the lake), that these areas are identifiable and measurable in a large lake, and that colonization of new spawning areas is related to the possibility of their discovery and subsequent use by dispersing lake trout. If these three concepts can be demonstrated, then identified spawning areas and those most likely to become colonized in the near future can be used as target areas for disrupting population expansion pathways for lake trout in Yellowstone Lake.

Goal, hypotheses, and objectives

Goal

The goal of this research was to identify potential lake trout spawning habitat sites in Yellowstone Lake, Yellowstone National Park, Wyoming.

Hypotheses

This research was driven by two hypotheses:

(1) Lake trout use small, distinct patches of identifiable, measurable habitat for spawning that are rare within Yellowstone Lake, and

(2) Identification of lake trout spawning sites with potential for colonization is possible from knowledge of spatial distributions of measurable habitat features.

Objectives

The specific objectives of this research were to:

(1) Describe physical habitat features at known lake trout spawning sites in Yellowstone and Lewis lakes, and

(2) Delineate spatial distribution pattern of potential spawning areas for lake trout throughout Yellowstone Lake.

Study Area

Yellowstone Lake, in north-western Wyoming, is a central feature of Yellowstone National Park. It has received a great deal of attention since the park was established in 1872 and was a frequent destination point for early travelers to the park, especially after the completion of Lake Yellowstone Hotel along the northern shore in 1890 (McCullen 2002). Early accounts report high-quality angling for native cutthroat trout.

Physical characteristics

At 2,357 m elevation and with surface area of about 34,000 ha, Yellowstone Lake has 239 km of shoreline (Kaplinski 1991) and is the largest high-altitude lake in North America. The watershed is approximately 261,590 ha and is dominated by lodgepole pine *Pinus contorta* and subalpine meadows

(Benson 1961). The upper Yellowstone River constitutes the largest in-flowing stream and represents 57.8% of the lake's watershed (Benson 1961). Mean depth of the lake is estimated to be 48.5 m (Kaplinski 1991). The deepest known point (133 m) is in a thermal vent southeast of Stevenson Island (Morgan et al. 2003). Yellowstone Lake is oriented along a 336^o azimuth with a maximum length of 32.8 km and maximum width of 25.8 km (Kaplinski 1991). The lake is generally ice-covered from mid-December until mid-May or early June (Gresswell et al. 1997). Water surface temperatures rarely exceed 18^oC (Gresswell and Varley 1988).

Yellowstone Lake generally experiences strong prevailing winds from the south southwest, generating surface currents toward the northeastern shore, bottom currents back to the southwest, and upwelling in the West Thumb (Benson 1961). The lake exhibits typical stratification with warming summer temperatures and has both fall and spring turnover.

Yellowstone Lake is exceptional in many ways, not the least of which is its geology. The lake lies primarily within the Yellowstone Caldera which was formed by two separate eruptions and subsequent collapses of magma chambers approximately 2.05 millium annum (Ma) and 0.64 Ma (Morgan et al. 2003). Southern portions of the lake outside the caldera were primarily influenced by glacial activity (Kaplinski 1991; Morgan et al. 2003). Underlying geology of Yellowstone Lake consists primarily of Tertiary andesitic rocks, pre-caldera and caldera-forming rhyolitic ignimbrites, post-collapse rhyolitic lava flows, and lake sediments (Morgan et al. 2003). The lake can be divided into one primary north-south oriented main basin and six secondary subbasins: Mary Bay, West Thumb, South Arm, Flat Mountain Arm, Breeze Channel, and an unnamed area south of the outlet into Yellowstone River (Figure 1-2; Kaplinski 1991).

West Thumb is the largest of these subbasins, and is thought to be the result of a separate collapsed caldera (165 kilo annum [ka]) within the Yellowstone Caldera. Connecting West Thumb to the Main Basin, Breeze Channel consists of a long trough-like basin extending east-northeast. Mary Bay subbasin occupies the central depression of a thermal explosion crater in the northeast section of the lake. Flat Mountain Arm and South Arm subbasins appear to have been formed primarily by glacier activity (Kaplinski 1991; Morgan et al. 2003).

Yellowstone Lake's bottom has many hydrothermal basins, fumaroles (hot gas vents), hydrothermal explosion craters (some greater than 500 m in diameter), fissures, hydrothermal spire structures (some over 30 m tall), landslide deposits, and active venting areas (Cuhel et al. 2002; Kaplinski 1991; Kaster et al. 1985; Morgan et al. 2003). These vents contribute to thermal and nutrient flows within the lake. Approximately 10% of the deep water flux for all of Yellowstone National Park occurs beneath Yellowstone Lake (Morgan et al. 2003). Anoxic hydrothermal waters are high in dissolved nutrients (carbonate, ammonium, silicate, phosphate, and sulfide) and support unique communities of life (Cuhel et al. 2002; Kaster et al. 1985). However, vents have also been reported to release high levels of potentially toxic materials such as Hg, Mo, Tl, As, Sb, and tungsten

(Cuhel et al. 2002; Morgan et al. 2003). Fumarole gases are primarily carbon dioxide with traces of methane and hydrogen sulfide (Kaster et al. 1985).

Hydrothermal activity occurs primarily in the northern section and West Thumb areas of the lake. Kaplinski (1991) reports vigorous hydrothermal upwelling along faults or fissures in Mary Bay and east of Stevenson Island (Figure 1-2). Mary Bay, formed by hydrothermal explosions subsequent to the formation of Yellowstone Lake (13.4 ka), is one of the most geothermally active areas of the lake (Wold et al. 1977). Many additional hydrothermal explosion craters have been documented below the surface of Yellowstone Lake, including areas east of the West Thumb geyser basin, southwest of Mary Bay, and south of Frank Island (Morgan et al. 2003). Many thermal vents have been mapped in the northern and West Thumb portions of Yellowstone Lake (Kaplinski 1991; Morgan et al. 2003).

Cuhel et al. (2002) suggested differing thermal domains in Yellowstone Lake based on chemical composition of inputs. For example, vents in the Mary Bay and Stevenson Island areas frequently contained high amounts of methane and hydrogen sulfide, which were rarely detected in the West Thumb vents. West Thumb vents, on the other hand, often had higher amounts of silicate than those in the northern areas of the lake.

Heat flow studies show Mary Bay and West Thumb have extremely high heat flux compared to other areas of the lake (Kaplinski 1991; Morgan et al. 2003). Morgan et al. (2003) report 35-m deep vent temperatures approaching 120 ^{o}C. Sediment temperatures at the substrate-water interface in Yellowstone Lake have been measured to be greater than 50°C while lake water was less than 16 °C (Kaster et al. 1985).

Other thermal features found extensively in Yellowstone Lake are anastomosing tubular structures formed in areas with diffuse hydrothermal vents (Figure 1-3). These structures are primarily silica precipitated when high-temperature vent fluids contact colder lake water. These structures can be found associated with both active and inactive vent areas in the northern, central, and West Thumb portions of Yellowstone Lake (Lisa Morgan, U.S. Geological Survey, personal communication).

Yellowstone Lake is an extremely dynamic system and subject to change. Lake water level apparently has a significant impact on hydrothermal activity, exerting its effect through changes in hydrostatic pressure above the magma chamber (Aguilar et al. 2002; Cuhel et al. 2002; Morgan et al. 2003), with increased activity accompanying decreased water levels. In the low water year of 1994, Cuhel et al. (2002) reported strong hydrogen sulfide odors in the entire lake area north of Stevenson Island, Mary Bay Beach was nearly too hot to walk on, and fumarole bubbles near Stevenson Island left rings of yellow-white material presumed to be elemental sulfur on the surface of the lake. They also found significant changes in vent water geochemistry when comparing their results with those obtained by Klump et al. (1988) a decade earlier.

Biotic characteristics

Although assumed to be oligotrophic, Theriot et al.'s (1997) analysis of 17 years of data suggested mesotrophic may be a more accurate classification of

Yellowstone Lake. Native fish include Yellowstone cutthroat trout and longnose dace *Rhinichthys cataractae*. Longnose suckers *Catostomus catostomus* also occur in the lake, are native to the park, but were historically restricted to areas downstream of the lake below Lower Yellowstone Falls (Behnke 1992; Varley and Schullery 1998). Other exotic fish species present in Yellowstone Lake include redside shiner *Richardsonius balteatus* and lake chub *Couesius plumbeus.* These species have been found in the lake since the 1920s (Gresswell and Varley 1988). Redside shiners, longnose dace, and lake chub all tend to be limited to shoreline, littoral areas, whereas longnose suckers occur throughout the lake. However, none of these species appear to have had negative effects on the native cutthroat trout (Gresswell and Varley 1988).

Yellowstone National Park encompasses 91% of the current range of Yellowstone cutthroat trout and contains 85% of the historic lake habitat for this subspecies (Gresswell 1995; Varley and Gresswell 1988). Current distribution of this subspecies is greatly reduced from its historic range. Declines have been attributed to hybridization with other cutthroat trout subspecies and rainbow trout *Oncorhynchus mykiss* (Gresswell 1995), aquatic habitat degradation (May 1996), whirling disease (Koel et al. 2006; Nehring and Walker 1996), excessive angler harvest (Gresswell and Varley 1988; Thurow et al. 1988), and introduction of exotic species (Varley and Schullery 1995a). These ongoing threats to remaining Yellowstone cutthroat trout populations led to a formal petition to list this subspecies as “threatened” throughout its range in 1998. Status is currently being reviewed and interagency conservation plans are being updated to attempt to halt further declines in the abundance and long-term viability of the subspecies.

In addition to being the largest population of Yellowstone cutthroat trout in existence, the Yellowstone Lake population is a valuable resource for several other reasons. Cutthroat trout play a significant role as both predator and prey in the Yellowstone Lake ecosystem and provide an important link to the terrestrial community as prey for numerous avian and mammalian predators and scavengers (Schullery and Varley 1995). Species such as the grizzly bear *Ursus horribilus*, mink *Mustela vison, and* otter *Lutra canadensis* seasonally seek cutthroat trout for a protein-rich diet source (Felicetti et al. 2004; Gresswell 1995; Haroldson et al. 2005; Mattson et al. 1991). Avian species, including bald eagle *Haliaeetus leucocephalus,* osprey *Pandion haliaetus,* and white pelican *Pelecanus occidentalis,* also rely on cutthroat trout as an important energy source (Davenport 1974; McEneaney 2002). McEneaney (2002) lists eleven additional avian species to which the Yellowstone cutthroat trout are important diet items.

A less visible impact of the establishment of the lake trout population and resultant reduction in the Yellowstone cutthroat trout population are changes in the lacustrine invertebrate community. Tronstad (2008) found a shift in the Yellowstone Lake zooplankton assemblage from a dominance of small copepods to that of large cladocerans. A decrease in phytoplankton with a concurrent increase in water clarity was also noted (Tronstad 2008). These changes are attributed to the addition of a trophic level within the system, changing the predator-prey dynamics, and causing a trophic cascade through the system (Tronstad 2008).

The cutthroat trout population in Yellowstone Lake supports a world-famous recreational fishery with an estimated value of more than $36 million to the regional economy in 1994 (Varley and Schullery 1995b). Anglers from all over the United States and from several foreign countries fish for these prized trout. Additionally, hundreds of thousands of people go out of their way annually to view these fish in their natural setting spawning and jumping cascades at Fishing Bridge and LeHardy's Rapids in Yellowstone National Park (Gresswell and Liss 1995).

Actual population size of Yellowstone Lake cutthroat trout has fluctuated considerably during the 20th century, primarily due to high levels of angler harvest and hatchery-related egg collections (Gresswell et al. 1994). Until recently, National Park Service (NPS) and U.S. Fish and Wildlife Service fishery managers believed negative impacts to the Yellowstone Lake cutthroat trout population were restricted to these influences. Closure of the hatcheries in the 1950's and numerous changes in angling regulations appeared to provide adequate protection to these fish up through the mid-1980s (Gresswell and Varley 1988). Indices such as increasing relative abundance, average size of spawning fish, and satisfactory catch rates by anglers provided evidence that the population had stabilized from previous overexploitation (Gresswell and Varley 1988).

However, when a lake trout was caught in Yellowstone Lake in July 1994, fishery biologists immediately became concerned about the future of the cutthroat trout population (Kaeding et al. 1996). A panel of experts from throughout the United States and Canada reviewed the situation and confirmed that without some type of intervention, a 70% or greater reduction in cutthroat trout abundance was highly probable within 50 to100 years (McIntyre 1995).

Following the discovery of lake trout, Yellowstone National Park committed to a removal program aimed at reducing the impact of lake trout to the cutthroat trout population (Bigelow et al. 2003; Mahony and Ruzycki 1997). Efforts have continued to intensify to counteract this nonnative threat (Koel et al. 2005). Each year, NPS staff has improved their knowledge of lake trout seasonal distribution patterns and their ability to target lake trout while avoiding by-catch of native cutthroat trout. In 2004, over 26,600 lake trout were removed from Yellowstone Lake (Figure 1-4). The ratio of cutthroat trout to lake trout sacrificed has remained low (one cutthroat trout lost for every 14-25 lake trout killed in 2003 and 2004). On a typical day during the open water season on Yellowstone Lake, approximately 16 km of gillnet were in place fishing for lake trout during the 2002-2004 field seasons (Koel et al. 2005).

Most effort has been directed at younger lake trout, which reside in deeper water than do most cutthroat trout, making use of gillnets viable. Larger lake trout tend to be less vulnerable to gillnets because of more sedentary life style and are often found at depths where the cutthroat trout by-catch is unacceptably high. However, mature lake trout show increased movements and congregate from late August until early October in preparation for spawning. This is a prime time to target the mature lake trout without harming an unacceptable number of cutthroat trout. Approximate locations of three suspected spawning areas in Yellowstone Lake are: (1) off Carrington Island, (2) west of the mouth of Solution Creek, and (3) northeast of West Thumb geyser basin (Figure 1-5). These areas have been targeted during the spawning season to capitalize on this behavior. In 2004, approximately 30% of the total number of lake trout removed were captured by focusing on spawning areas during spawning season (Koel et al. 2005).

Despite this control effort, large numbers of lake trout remain in Yellowstone Lake, and the population appears to be expanding. The number of mature lake trout removed from or near spawning areas reached a record high in 2004 at 8,346 fish (Figure 1-6, Bigelow unpublished data). This immediately followed another record of 2,373 lake trout caught in or near spawning areas during 2003. Part of the increase (almost 20% of the catch both years) can be attributed to the newly identified spawning area near West Thumb geyser basin. Also, a small number (1.4%) of lake trout caught near spawning areas are immature, apparently there to opportunistically feed on their kin's eggs. Those facts notwithstanding, an increase in the spawning population of lake trout in Yellowstone Lake appears to be occurring. Despite some encouraging trends (decreased mean size, increased percentage of young spawners, continued low catch rates throughout the majority of the lake; Koel et al. 2005), the question remains: Are lake trout removal efforts enough to allow recovery of Yellowstone cutthroat trout in the lake?

Lake trout

Lake trout are capable of voracious piscivory, and hence are a serious threat to Yellowstone cutthroat trout in Yellowstone Lake. As a relatively new species to the system (Kaeding et al. 1996; Munro et al. 2005; Ruzycki et al. 2003), the lake trout population probably has not reached equilibrium with its environment and may be exhibiting substantial population expansion. Despite serious efforts to reduce this population within Yellowstone Lake (Bigelow et al. 2003; Koel et al. 2005), numbers of mature adults caught on or near known spawning areas has increased almost exponentially over the last few years (Figure 1-6). Lake trout exhibit spawning behavior that is unique among salmonids and may present a life history trait exploitable for controlling population expansion. Unlike most salmonid species, lake trout do not pair for spawning or construct redds for the protection of their eggs and young (Scott and Crossman 1973). Instead, they exhibit group, broadcast spawning over specific sites. Two aspects of this behavior will likely contribute to control of their population numbers: (1) the need to congregate in groups prior to and during spawning, and (2) the specific habitat choice for physical protection, embryo oxygenation, and removal of waste products from the developing embryo. These two factors likely limit the array of spawning sites for lake trout in a lake system.

If patches of suitable spawning habitat can be identified in Yellowstone Lake, then an alternative approach to control the population, both by removing concentrated numbers of mature lake trout or by interrupting recruitment to the population, may be viable. Prohibition or limiting reproduction, hatch of embryos, or fry escapement are all prospective means of interrupting recruitment.

Mature lake trout are widely dispersed throughout Yellowstone Lake (Maiolie 1998; Ruzycki et al. 2003). Capture of fish by passive gear, such as a gillnet, is limited by the movements of the fish. If they are not moving, they will not become entangled and captured. Mature lake trout, which have switched their diet from invertebrates to fish, will likely demonstrate much less and much more sporadic movements, making them difficult to target for capture. Digestion time for a relatively large fish, such as a cutthroat trout, is much greater than for smaller invertebrates, theoretically negating the need for that lake trout to continue searching until digestion is completed, presumably leading to less and more sporadic movements.

Habitat and range.—Lake trout have a native range from Alaska through Canada, the Great Lakes region, and parts of Montana (Martin and Olver 1980; Oswald and Snyder 2005). They are an important economic species and considered a desirable food and sport fish (Martin and Olver 1980). Because of their desirability they have been widely introduced into lakes in western North American (Martin and Olver 1980; Scott and Crossman 1973).

Typically considered a deep, cold water species, they are often found in shallow areas of lakes and in rivers in the northern portions of their range (Martin and Olver 1980). Preferred water temperatures range from 10.8 to 12.7^{o}C (Christie and Regier 1988). Thermal stratification during summer is thought to limit lake trout movements because water temperatures in the epilimnion often exceed thermal preferences. However, even in the more southern portions of their range, which would include Yellowstone Lake, they can be captured in shallow waters when temperatures are cold, such as just after ice-off or during their fall spawning activities (Martin and Olver 1980; Scott and Crossman 1973), or when making feeding forays into the warmer epilimnion of the lake.

Given the plasticity of lake trout and the diversity of habitats they reside in, study of specific life history traits has been difficult (Martin and Olver 1980). The catastrophic declines in lake trout populations in the Great Lakes, however, fueled research on this species and its life history traits (Martin and Olver 1980).

Spawning behavior.—Spawning occurs in the fall and several factors are thought to influence its initiation and duration. Specific spawning time is influenced by latitude, weather, and size and topography of the lake (Scott and Crossman 1973). Declining water temperatures to approximately 10°C (MacLean et al. 1990; Martin and Olver 1980), shortening photoperiod and accumulated sunlight (McCrimmon 1958; Royce 1951), and wind activity, both intensity and duration (Martin 1957), all appear to be important in stimulating lake trout to migrate to spawning areas and to trigger spawning activities. In addition, wind activity and accumulated sunlight appear to affect the duration of spawning. Strong, prolonged winds can trigger spawning and quickly lead to its completion, while prolonged bright, calm days have been implicated in more prolonged spawning activity (Martin and Olver 1980).

Mature lake trout have been reported to congregate in ‘staging’ areas before the actual onset of spawning activities. The use of “staging areas” is often mentioned in the literature (Martin and Olver 1980) but not well documented. Several characteristics of lake trout spawning activities, such as group spawning, broadcast spawning, and aversion to light, make it reasonable to expect that they would congregate in preparation for spawning. Traditional thought suggests that lake trout gather in areas of deep water near spawning areas in preparation for spawning. Depth provides appropriate temperature and cover from sunlight. After darkness, lake trout move onto the spawning area and remain there for several hours. Perhaps pheromones from mature fish present help attract others to the area (Johnson et al. 2005).

Gillnet catches in Yellowstone Lake lend support to the use of ‘staging areas.’ Nets set in areas in close proximity to known spawning sites typically produce high numbers of ripe lake trout prior to the onset of spawning, showing an increased movement of mature lake trout in the vicinity (Bigelow, unpublished data).

Males are thought to remain in the vicinity of spawning areas for several days or weeks, likely spawning multiple times throughout the season. Females are also believed to move in and out of spawning areas repeatedly during the spawning season. However, it is not known if they do this in preparation for spawning and leave after spawning once or if they will emit eggs on multiple occasions (Martin and Olver 1980).

Male-to-female ratio of lake trout captured on or near spawning areas is typically heavily skewed toward males, supporting the theory that males remain on spawning grounds for a longer period of time (Martin 1957; Martin and Olver

1980). Males typically reach maturity at a younger age than females and migrate to spawning areas ahead of the females both annually and daily (Martin and Olver 1980), which would also contribute to the skewed sex ratio.

Specific habitat requirements for spawning.—Specific habitat structure is critical to the reproductive success of lake trout. Factors such as wave action, fetch, wind energy, and substrate size and resultant interstitial spaces work in combination to provide adequate conditions for developing embryos. Lake trout make no attempt to bury eggs or to guard them (Martin and Olver 1980). Eggs are negatively buoyant and descend into interstitial spaces in the substrate. This behavior makes the choice of spawning site critical to the survival of the offspring.

Reported substrate sizes used by lake trout for spawning vary greatly. Scott and Crossman (1973) reported lake trout spawning to occur most often over large boulder or rubble substrate. In the Great Lakes, Edsall and Kennedy (1995) examined five known spawning areas and found the best substrate available for lake trout spawning at each site ranged from gravel (2 to 64 mm) to fractured bedrock with loose rocks scattered on the surface.

Reported spawning depths also range widely in the literature. In small- to medium-sized inland lakes, depths tend to be shallow. Scott and Crossman (1973) reported spawning generally occurred at depths less than 12 m. Flavelle et al. (2003) observed (via telemetry) mature lake trout in Lake Opeongo, Ontario using areas of 1.7-8.4 m depth during what were believed to be spawning activities. After reviewing data from 95 inland Ontario lakes with 281 known spawning sites, MacLean et al. (1990) recommended searching for new spawning areas in depths less than 4 m deep. However, lake trout spawning has been reported to occur at depths as great as 55 m (Martin and Olver 1980).

Interstitial spaces within the substrate are another important attribute of spawning substrate. Substrate must exhibit a high proportion of cracks and crevices to allow eggs to sink into interstitial spaces. Interstitial spaces are thought to provide physical protection from predators. They must also allow for adequate water flow for eggs to remain aerated and toxin free.

Slope, substrate size and angularity, depth of interstitial spaces, wind fetch, water temperature, prevailing wind directions, and dissolved oxygen are all important variables to lake trout when choosing a spawning site (Edsall and Kennedy 1995; Kelso et al. 1995; MacLean et al. 1990; Martin and Olver 1980; Scott and Crossman 1973). More importantly, it appears it is the interaction of these variables that is driving creation of suitable spawning and incubation conditions for developing embryos. Water movement is important to the developing embryos in order to provide adequate oxygenation and remove metabolic wastes. Structure stability is important to provide protection from crushing.

Rowan et al. (1992) theorized that by using wave energy and particle threshold dynamics, they could predict the boundary between low-energy, deposition zones with accumulated fine-grained cohesive sediments and high-energy, erosive zones with coarse-grained non-cohesive sediments. After developing a relation using fetch and exposure, coupled with local wind activity, as separate surrogates for maximum wave height, they used observations from sites at over 50 lakes in Quebec and Ontario, including lakes as small as 10 km^2 and as large as Lake Superior (82,367 km^2) to test their equation. They determined slope also had a significant effect on the location of the boundary between these zones and that maximum wave height over predicted the actual depth of erosion and empirically adjusted their function to accommodate these factors. Their final model correctly classified deposition and erosive zones 87% and 70% of the time. The model, using fetch as the surrogate for maximum wave height is:

$$\text{Log DBD} = -0.107 + 0.742 * \log F + 0.06 + 0.0653 * S \text{ where,}$$

DBD = the deposition boundary depth between erosion and deposition (m),
F = fetch along the longest axis, and
S = slope (%).

Adapting this function, Flavelle et al. (2002) suggested lake trout take advantage of the areas developed by the dynamics of wave action, to choose sites with appropriately aerated and cleaned substrate. They predicted spawning sites in Lake Opeongo would occur within either the erosive zone or a transition area 1 m depth either side of the estimated boundary, and termed this area the transition zone. They adapted the equation by using only weather data during lake trout spawning activity (in their case, October) to define fetch as maximum distance to shore along the prevailing wind direction. Locations of all known spawning sites in Lake Opeongo were found within the lake’s transition or erosive zones.

References

Aguilar, C., R. Cuhel, and J. V. Klump. 2002. Porewater and hydrothermal vent water inputs to Yellowstone Lake, Wyoming. Pages 1-18 *in* R. J. Anderson, and D. Harmon, editors. Yellowstone Lake: hotbed of chaos or reservoir of resilience? Yellowstone Center for Resources and The George Wright Society, Yellowstone National Park, Wyoming and Hancock, Michigan.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Non-native stream fish invasion restructures stream and riparian forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656-2663.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Bethesda, Maryland.

Behnke, R. J. 2002. Trout and Salmon of North America. The Free Press, New York, NY.

Benson, N. G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Research Report 56:33.

Bigelow, P. E., and five coauthors. 2003. Protection of native Yellowstone cutthroat trout in Yellowstone Lake, Wyoming. Final Report. Technical Report NPS/NFWRD/NRTR-2003/314. 12 pages.

Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalization of alien recreational freshwater fisheries. Hydrobiologia 500:217-230.

Christie, G. C., and H. A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences 45:301-314.

Cordone, A. J., and T. C. Frantz. 1966. The Lake Tahoe sport fishery. California Fish and Game 52:240-274.

Crockett, H. J. 2004. Assessment of lake trout abundance and ecology in a Colorado reservoir using hydroacoustic and mark-recapture techniques. M.S. Thesis, Colorado State University. Fort Collins, Colorado. 128 pages.

Cuhel, R., and seven coauthors. 2002. Underwater domains in Yellowstone Lake hydrothermal vent geochemistry and bacterial chemosynthesis. Pages 27-53 *in* R. J. Anderson, and D. Harmon, editors. Yellowstone Lake: hotbed of chaos or reservoir of resilience? 6th Biennial Scientific Conference on the Greater Yellowstone Ecosystem. Yellowstone Center for Resources and The George Wright Society, Mammoth Hot Springs, Yellowstone National Park, Wyoming.

Davenport, M. 1974. Piscivorous avifauna on Yellowstone Lake, Yellowstone National Park. Montana State University, Bozeman, Montana.

Dean, J., and J. D. Varley. 1974. Fishery management investigations. Yellowstone National Park, Bureau of Sport Fisheries and Wildlife, Technical Report for 1973., Yellowstone National Park, Wyoming.

Deleray, M., L. Knotek, S. Rumsey, and T. Weaver. 1999. Flathead Lake and River System Fisheries Status Report. Montana Fish, Wildlife, and Parks, Kalispell, Montana.

Edsall, T. A., and G. W. Kennedy. 1995. Availability of lake trout reproductive habitat in the great lakes. Journal of Great Lakes Research 21(SUPPL. 1):290-301.

Felicetti, L. A., and seven coauthors. 2004. Use of naturally occurring mercury to determine the importance of cutthroat trout to Yellowstone grizzy bears. Canadian Journal of Zoology 82(3):493-501.

Flavelle, L. S. 2003. A description of space use and habitat selection in Lake Opeongo lake trout *Salvelinus namaycush*. Master of Science thesis. University of Waterloo, Waterloo, Ontario, Canada.

Flavelle, L. S., M. S. Ridgway, T. A. Middel, and R. S. McKinley. 2002. Integration of acoustic telemetry and GIS to identify potential spawning areas for lake trout *Salvelinus namaycush*. Hydrobiologia 483:137-146.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36-54 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. USDA Forest Service General Technical Report RM-GTR-256.

Gresswell, R. E., H. Li, and P. Rossignol. 1997. Ecological risk analysis of a piscivorous fish introduction into the Yellowstone Lake ecosystem. Wild Trout VI:122-126.

Gresswell, R. E., and W. J. Liss. 1995. Values associated with management of Yellowstone cutthroat trout in Yellowstone National Park. Conservation Biology 9:159-165.

Gresswell, R. E., W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhychus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51 (Supplement 1):298-309.

Gresswell, R. E., and J. D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. Pages 45-52 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout, volume 4. American Fisheries Society, Bethesda, Maryland.

Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution 19(9):470-474.

Haroldson, M. A., and seven coauthors. 2005. Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bear visiting streams from DNA. Ursus 16(2):167-180.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:115-131.

Johnson, N. S., M. J. Siefkes, and W. Li. 2005. Capture of ovulating female sea lampreys in traps baited with spermiating male sea lampreys. North American Journal of Fisheries Management 25:67-72.

Kaeding, L. R., G. D. Boltz, and D. G. Carty. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries 21(3):16-20.

Kaplinski, M. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. Northern Arizona University.

Kaster, J. L., J. V. Klump, and C. C. Remsen. 1985. Sub-lacustrine fumarole communities in Yellowstone Lake: naturally occurring hydroponic system. Final Report. Center for Great Lakes Studies.

Kelso, J. R. M., W. R. MacCallum, and M. L. Thibodeau. 1995. Lake trout spawning at five sites in Ontario waters of Lake Superior. Journal of Great Lakes Research 21(SUPPL. 1):202-211.

Klump, J. V., C. C. Remsen, and J. L. Kaster. 1988. The presence and potential impact of geothermal activity on the chemistry and biology of Yellowstone Lake, Wyoming. Pages 81-98 *in* M. DeLuca, and I. Babb, editors. Global venting, midwater and benthic ecological processes. NOAA Symposium on Undersea Research, NOAA.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative Lake Trout Result in Yellowstone Cutthroat Trout Decline and Impacts to Bears and Anglers. Fisheries 30(11):10-19.

Koel, T. M., and six coauthors. 2006. *Myxobolus cerebralis* in native cutthroat trout of the Yellowstone Lake ecosystem. Journal of Aquatic Animal Health 18:157-175.

Luecke, C., M. W. Wengert, and R. Schneiderven. 1999. Comparing results of a spatially explicit growth model with changes in the length-weight relationship of lake trout *Salvelinus namaycush* in Flaming Gorge Reservoir. Canadian Journal of Fisheries and Aquatic Sciences 56 Supplement:162-169.

MacLean, N. G., and six coauthors. 1990. Environmental and genetic factors affecting the physiology and ecology of lake trout. Lake trout synthesis, Physiology and Ecology Working Group. Ontario Ministry of Natural Resources. Toronto.

Mahony, D. L., and J. R. Ruzycki. 1997. Initial investigations towards the development of a lake trout removal program in Yellowstone Lake. Wild Trout VI symposium:153-162.

Maiolie, M. A. 1998. Hydroacoustic search for lake trout in Yellowstone Lake, 1997. Idaho Department of Fish and Game, Coeur d'Alene, Idaho.

Maiolie, M. T., T. Bassista, and M. Peterson. 2005. Lake Pend O'Reille Quarterly Report, October-December, 2004. Idaho Fish and Game Department, Boise, Idaho.

Marnell, L. F. 1986. Impacts of hatchery stocks on wild fish populations. American Fisheries Society, Bethesda, Maryland.

Martin, N. V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. Transactions of the American Fisheries Society 86:231-244.

Martin, N. V., and C. H. Olver. 1980. The lake charr *Salvelinus namaycush*. Pages 205-277 *in* E. K. Balon, editor Charrs: salmonid fishes of the genus *Salvelinus*. Kluwer Boston, Inc., Hingham, Massachusetts.

Martinez, P. J., and nine coauthors. in review. Western lake trout woes. Fisheries.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears. Canadian Journal of Zoology 69:1619-1629.

May, B. 1996. Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*. USDA Forest Service General Technical Report RM-GTR-256.

McCrimmon, H. R. 1958. Observations on the spawning of lake trout, *Salvelinus namaycush*, and the post-spawning movement of adult trout in Lake Simcoe. Canadian Fish Culturist 23:3-11.

McCullen, M. 2002. An archeological investigation of a historic refuse dump associated with the Yellowstone Lake Hotel. Pages 114-120 *in* R. J. Anderson, and D. Harmon, editors. Yellowstone Lake: hotbed of chaos or reservoir of resilience? Yellowstone National Park and the George Wright Society, Mammoth Hot Springs, Yellowstone National Park, Wyoming.

McEneaney, T. 2002. Piscivorous birds in Yellowstone Lake: their history, ecology, and status. Pages 121-134 *in* R. J. Anderson, and D. Harmon, editors. Yellowstone Lake: hotbed of chaos or reservoir of resilience? Yellowstone Center for Resources and The George Wright Society, Yellowstone National Park, Wyoming and Hancock, Michigan.

McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout, Proceedings of a workshop and information exchange held in Gardiner, Montana, February 15-17, 1995. The Yellowstone Lake crisis: confronting a lake trout invasion. A Report to the Director of the National Park Service:28-36.

Morgan, L. A., and 13 coauthors. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 122:221-242.

Munro, A. R., T. E. McMahon, and J. R. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush)* in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sicence 62:79-87.

Nehring, R. B., and P. G. Walker. 1996. Whirling disease in the wild: the new reality in the Intermountain West. Fisheries 21(6):28-30.

Normile, D. 2004. Expanding trade with China creates ecological backlash. Science 306:968-969.

Oswald, D., and B. Snyder. 2005. Status of native lake trout in Montana. www.fisheries.org/AFSmontana/SSCpages/Lake%20Trout%20Status%Paper.htm.

Quist, M. C., and W. A. Hubert. 2004. Bioinvasive species and the preservation of cutthroat trout in the western United States: ecological, social, and economic issues. Environmental Science & Policy 7:303-313.

Rowan, D. J., K. J., and R. J. B. 1992. Estimating the mud deposition boundary depth in lakes from wave theory. Canadian Journal of Fisheries and Aquatic Sciences 49:2490-2497.

Royce, W. F. 1951. Breeding habits of lake trout in New York. U.S. Fish and Wildlife Fisheries Bulletin 52:59-76.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah-Idaho. Transactions of the American Fisheries Society 130:1175-1189.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folkes, and B. Walker. 2001. Catastropic shifts in ecosystems. Nature 413:591-596.

Schullery, P., and J. D. Varley. 1995. Cutthroat trout and the Yellowstone Lake ecosystem. The Yellowstone Lake Crisis: Confronting a Lake Trout Invasion, A Report to the Director of the National Park Service:12-21.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada Bulletin 184(Lake Trout *Salvelinus namaycush* (Walbaum)):220-229.

Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. Frontiers in Ecology and the Environment 3:12-20.

Theriot, E. C., S. C. Fritz, and R. E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park. Alpine and Arctic Research 29:304-314.

Thurow, R. F., C. E. Corsi, and V. K. Moore. 1988. Status, ecology, and management of Yellowstone cutthroat trout in the Upper Snake River drainage, Idaho. American Fisheries Society Symposium 4:25-36.

Tronstad, L. M. 2008. Ecosystem consequences of declining Yellowstone cutthroat trout in Yellowstone Lake and spawning streams. PhD, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, May 2008.

Varley, J. D., and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. American Fisheries Society Symposium 4:13-24.

Varley, J. D., and P. Schullery. 1995a. Executive Summary. The Yellowstone Lake crisis: confronting a lake trout invasion, A report to the director of the National Park Service. National Park Service, Yellowstone National Park, Wyoming.

Varley, J. D., and P. Schullery. 1995b. Socioeconomic values associated with the Yellowstone Lake cutthroat trout. The Yellowstone Lake crisis: confronting a lake trout invasion. A Report to the Director of the National Park Service:22-27.

Varley, J. D., and P. Schullery. 1998. Yellowstone Fishes. Ecology, history, and angling in the park, 2nd edition. Stackpole Books, Mechanicsburg, Pennsylvania.

Wold, R. J., M. A. Mayhew, and R. B. Smith. 1977. Bathymetric and geophysical evidence for a hydrothermal explosion crater in Mary Bay, Yellowstone Lake, Wyoming. Journal of Geophysical Research 82:3733-3738.

Wydoski, R. S., and R. W. Wiley. 1999. Management of undesirable fish species, Pages 403-430 *in* C. C. Koehler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Yule, D. L., and C. Luecke. 1993. Lake trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Transactions of the American Fisheries Society 122:1058-1069.

PHYSICAL HABITAT FEATURES AT SUSPECTED LAKE TROUT SPAWNING SITES IN YELLOWSTONE LAKE

The recent illegal introduction and population expansion of lake trout *Salvelinus namaycush* in Yellowstone Lake, Wyoming has had detrimental effects on the native Yellowstone cutthroat trout *Oncorhynchus clarki boueveri* (Kaeding et al. 1996; Koel et al. 2005; Munro et al. 2005; Ruzycki et al. 2003). The National Park Service (NPS) has made suppression of this non-native population a high-priority resource issue and continues to advocate its suppression (Koel et al. 2007) in an attempt to protect Yellowstone cutthroat trout. As part of the suppression program, the NPS has found adult lake trout to be particularly vulnerable to removal efforts during spawning season (Bigelow et al. 2003).

Specific habitat structure is critical to the reproductive success of lake trout. Factors such as wave action, fetch, wind energy, and substrate size and resultant interstitial spaces work in combination to provide adequate conditions for developing embryos. Lake trout make no attempt to bury or guard eggs (Martin and Olver 1980). This behavior makes the choice of spawning site critical to the survival of the offspring.

Substrate sizes used by lake trout for spawning vary greatly. Scott and Crossman (1973) reported lake trout spawning to occur most often over large boulder or rubble substrate. In the Great Lakes, Edsall and Kennedy (1995) examined five known spawning areas and found the best substrate available for lake trout spawning at each site ranged from gravel (2 to 64 mm) to fractured bedrock with loose rocks scattered on the surface. In Lake Tahoe lake trout were documented using deepwater macrophyte beds (Beauchamp et al. 1992).

Spawning depths also range widely. In small- to medium-sized inland lakes, depths tend to be shallow. Scott and Crossman (1973) reported spawning generally occurred at depths less than 12 m. Flavelle et al. (2003) observed mature lake trout in Lake Opeongo, Ontario using areas of 1.7-8.4 m depth during what were believed to be spawning activities. MacLean et al. (1990) recommended searching for new spawning areas in depths less than 4 m deep. However, lake trout spawning has been reported to occur at depths as great as 55 m in Lake Tahoe (Beauchamp et al. 1992) and 91 m in Lake Superior (Martin and Olver 1980). In general, increasing spawning depth seem to occur with increasing lake size (Martin 1957).

Water quality is an important characteristic of potential spawning areas. High water temperature, low dissolved oxygen, and presence of toxic substances are all factors which could limit embryo and fry survival (Martin and Olver 1980; Piper et al. 1982; Scott and Crossman 1973; Sly 1988).

Interstitial spaces within the substrate are another important attribute of spawning location. Literature strongly supports interstitial space of adequate depth is essential to provide protection and shelter to developing embryos (Biga et al. 1998; Edsall et al. 1998; Fitzsimons 1995; Kelso et al. 1995; Marsden et al. 1995), however, it can be difficult to judge (Gunn et al. 1996). Eggs are negatively buoyant and descend into these interstitial spaces in the substrate. Substrate must exhibit a high proportion of cracks and crevices to allow eggs to sink into interstitial spaces. These spaces are thought to provide physical protection from predators (Biga et al. 1998). They must also allow for adequate water flow for eggs to remain aerated and toxin free.

Additionally, the underlying geologic formation of the lake substrate may offer insight into the water-substrate interface available to lake trout. For example, andesite, rhyolite, lake sediments, hydrothermal explosion deposits, alluvium, landslides, glacial deposits, and tuff constitute the major classes of Yellowstone Lake's underlying geologic formations (Morgan et al. 2003). Perhaps some of these classes are more prone to providing clean, fractured or angular layers of substrates which would provide lake trout spawning habitat.

Rowan et al. (1992) theorized that by using wave energy and particle threshold dynamics, they could predict the boundary between low-energy, deposition zones with accumulated fine-grained cohesive sediments and high-energy, erosive zones with coarse-grained non-cohesive sediments. Rowan et al. (1992) developed a relation using fetch length coupled with local wind activity as a surrogate for maximum wave height, to predict the boundary between deposition and erosive zones within lakes. After testing their predictions with observations from sites at over 50 lakes in Quebec and Ontario, including lakes as small as 10 km^2 and as large as Lake Superior (82,367 km^2, they determined slope also had a significant effect on the location of the boundary between these zones and that maximum wave height over predicted the actual depth of erosion and empirically adjusted their function to accommodate these factors. Their final model correctly classified deposition and erosive zones 87% and 70% of the time. The model, using fetch length as the surrogate for maximum wave height is:

$$\text{Log DBD} = -0.107 + 0.742 * \log F + 0.0653 * S \text{ where,}$$

DBD = the deposition boundary depth between erosion and deposition (m),
F = fetch along the longest axis, and
S = slope (%).

Adapting this function, Flavelle et al. (2002) suggested lake trout take advantage of the areas developed by the dynamics of wave action, to choose sites with appropriately aerated and cleaned substrate. They predicted spawning sites in Lake Opeongo would occur within either the erosive zone or a transition area 1 m depth on either side of the estimated boundary, and termed this area the transition zone. They adapted the equation by using only weather data during lake trout spawning activity (in their case, October) to define fetch as maximum distance to (Martin and Olver 1980) shore along the prevailing wind direction. Locations of all known spawning sites in Lake Opeongo were found within the lake's transition or erosive zones.

Thus, slope, substrate size and angularity, depth of interstitial spaces, fetch length, water temperature, prevailing wind directions, and dissolved oxygen all appear to be important variables to contributing to successful lake trout spawning site selection (Edsall and Kennedy 1995; Kelso et al. 1995; MacLean et al. 1990; Martin and Olver 1980; Scott and Crossman 1973). More importantly, it appears it is the interaction of these variables that is driving creation of suitable spawning and incubation conditions for developing embryos. Water movement is important to the developing embryos in order to provide adequate oxygenation and remove metabolic wastes. Structure stability is important to provide protection from crushing.

Mature lake trout have been reported to congregate in ‘staging’ areas before the actual onset of spawning activities. The use of ‘staging areas’ is mentioned in the literature (Martin and Olver 1980). Several characteristics of lake trout spawning activities, such as group spawning and broadcast spawning, make it reasonable to expect that they would congregate in preparation for spawning (DeRoche 1969; Edsall and Kennedy 1995; Gunn 1995; Martin and Olver 1980). Traditional thought suggests that lake trout gather in areas of deep water near spawning areas in just prior to and during the spawning season. Perhaps pheromones from mature fish present help attract others to the area as well (Johnson et al. 2005; Young 2001).

It is widely accepted that lake trout using shallow, rocky substrate for spawning move into these areas after dark (Martin and Olver 1980). After darkness, lake trout move onto the spawning areas and remain there for several hours (personal observation; Gunn 1995; Martin and Olver 1980). However, lake trout are rarely seen over these areas, particularly on bright days, during daylight hours (Martin and Olver 1980). Shallow spawning areas often are located near deep water (Martin and Olver 1980) where depth can provide appropriate temperature and daylight cover. This suggests proximity to deeper water may be an important feature of lake trout spawning habitat, perhaps providing pre-spawning staging areas. Therefore, distance to refuge (e.g. 20- to 30-m deep water) could potentially be an important variable for spawning site selection. However, actual depths lake trout return to during daylight hours is not defined in the literature. Anecdotal information from gillnetting efforts on Yellowstone Lake suggests that it is greater than 20 m (Brian Ertel, National Park Service, Yellowstone National Park, personal communication).

The National Park Service (NPS) has identified three areas in the West Thumb of Yellowstone Lake suspected to be lake trout spawning areas, as evidenced by high catches of lake trout physiologically preparing to spawn over multiple years of removal efforts (Figures 2-1 and 2-2; Koel et al. 2005). Available data suggest that the Carrington Island site has been in use at least since 1996 (Ruzycki 2004) and is where most mature lake trout have been captured during NPS removal efforts (Figures 2-3 and 2-4). Preliminary examination of the area indicated that adult lake trout choose shallow (< 2 m), clean (sediment free) gravel-rubble areas for spawning at each end of the island. The other two suspected sites, Solution Creek in the southeast portion of West Thumb and an area near West Thumb Geyser basin (Figure 2-1), are located in water up to 20 m deep with unknown substrate.

This study was designed to gain understanding of lake trout spawning habitat in Yellowstone Lake, and as a step toward mapping potential spawning habitat throughout the lake. To accomplish this we obtained detailed information regarding the location of suitable spawning substrate and the physical features associated with these locations within each of the three suspected lake trout spawning areas.

Three objectives were used to describe the habitat characteristics at the three suspected spawning areas: (1) view substrate structure at each suspected site, (2) use these observations to delineate specific polygons of suitable spawning habitat substrate based on presence of sediment-free, angular, rocky substrate, and (3) measure and summarize additional features of the habitat which occurred within boundaries of each of these spawning habitat polygons.

Methods

Underwater videography

A tool in recording substrate present at each area for analysis was underwater videography (Appendix A). The camera used was a miniature color underwater television camera with a titanium pressure housing, 2.9 mm fixed focus (15.2 cm to infinity), wide angle lens (model Aurora purchased from Insite Pacific Inc., Solana Beach, CA). By mounting it to a sled, it could be towed via cable by a motorboat along pre-determined transects in areas of interest. By weighting the sled and operating the boat at minimum speeds, the camera was kept under the boat so that the on-board Global Position System (GPS) unit could be used to determine location. Depth of the camera was controlled by a cable and winch mounted in the bow of the vessel and was kept above the substrate bottom so as not to interfere or become entangled with benthic or substrate materials, yet close enough to keep the camera view in focus, generally between 0.5 and 2.0 m.

The towed sled was equipped with two lasers, mounted a known distance apart, and an underwater light (Figure 2-5). Reflections of red light from the lasers, seen as red dots in the view, were used as a size reference for objects in the view. Data from the boat's onboard sonar and GPS were overlaid as text on the video frame as it was recorded, providing a permanent record of GPS location (Universal Transverse Mercator, North American Datum 1983, Zone 12N), date, time, and any user-provided text for each data frame (usually transect identification). Post-processing of the videography involved freezing the video stream at selected points, recording to file a "snapshot" of the image and entering the overlain data (location, date, and time) to a database for further analysis. Area covered by each snapshot varied dependent on camera height above the substrate. Typical snapshots covered an area approximately 2.25 m^2, but ranged from 0.2-2.0 m^2.

View substrate at suspected spawning areas

Three areas in the West Thumb portion of Yellowstone Lake were selected for detailed observation (Figure 2-1). Based on gillnet catch data of ripe lake trout during spawning season, a general boundary was developed for each of these areas (Figure 2-2). Transects within each area were designated to systematically cover the area. Where angular, rocky substrates were observed, additional transects were conducted in order to obtain more detailed information on the extent of that substrate. Actual boat path varied from the designated transects due to boat handling imprecision.

At Carrington Island, known spawning habitat in the form of rubble occurred at each end of the island (Figure 2-4; personal observation). Videography for this site began in water over substrate not suitable for spawning (fine sediment or vegetation) and was collected shoreward. Twelve beginning points surrounded the island and transects were run toward shore until shallow depth prevented the camera from remaining underwater (about 0.5 m depth; Figure 2-6). Videography was collected along 4 additional transects in areas where sediment-free, angular rubble and large gravel were observed for detail on the extent of the substrate (Figure 2-7). These transects were zigzagged over the area of interest.

Fifteen transects were designated at the site near West Thumb geyser basin (Figure 2-8). These sites had beginning points approximately equidistance apart and were run toward a single central point in order to cover the area where NPS gillnets caught high numbers of ripe lake trout (Koel et al. 2005). Thirteen additional transects were conducted in areas where rocky substrate was noted (Figure 2-9).

For the spawning site near the mouth of Solution Creek, five transects were selected to run approximately parallel to each other and another five were selected perpendicular to the first group (Figure 2-10). Four additional transects were conducted in the Solution Creek area to provide more intensive data collection in areas where potential suitable substrate might exist (Figure 2-11).

All videos were viewed and subsampled (by extracting video frames to snapshots) to determine extent of rocky substrates which could contribute to potential spawning habitat. Initial screening of the videos involved extracting snapshots at least every two minutes (typically 20-40 m apart) and at points where a change in substrate type was noted.

Substrate size was measured from the extracted video data frames, or snapshots. Primary substrate size was classified according to the dominant matrix present (most prevalent substrate size). Five measured classes were used (modified from Edsall et al. 1998): sand, fines, or vegetation (< 2 mm in diameter or presence of vegetation), gravel (2-64 mm), rubble (65-256 mm), cobble (257-999 mm), and boulder (>999 mm). Measurements were made along the longest axis of the substrate particle.

Other substrate classes also used where particle sizes were not measured were bedrock and thermal features. Both of these classes may or may not be suitable for spawning habitat depending on other features. For example, bedrock with high angularity and fractures could constitute suitable habitat (Edsall and Kennedy 1995). Inactive thermal features exhibiting high amounts of anastomosing tubular structures (Figure 2-12) could also provide good spawning substrate. When mixed substrates were present, a secondary substrate size, based on the second most common substrate present, was classified using the same categories.

Interstitial spacing was classified to 0-5%, 5-25%, 25-50%, 50-75%, or 75-100% based on the classifier's judgment of the amount of infilling (with fines, sand, or detritus) of interstitial spaces present. In snapshots where either the primary or secondary substrate present was sand, fines, or vegetation, interstitial spacing was classified as not applicable (NA).

Videos where rocky substrate were observed were viewed a second time with more detailed data extraction to delineate boundaries of areas with clean, angular rock (gravel, rubble, or cobble).

Delineate boundaries of known spawning sites

The next step toward characterizing habitat features at areas where suitable spawning substrate exists within Yellowstone Lake was to use the collected data to specify spawning substrate boundaries within the suspected areas. Each snapshot was reclassified to incorporate substrate type and interstitial spacing present into one variable indicating suitable spawning substrate (Table 2-1). Location of all snapshots were mapped into a Geographic Information System (GIS) and displayed as ‘none’, ‘marginal’, or ‘present’ as described below.

Areas not expected to provide adequate lake trout spawning substrate were mapped as ‘none’. These included all snapshots classified with the primary substrate present as vegetation, sand, or silt, and all snapshots where very little interstitial space existed between whatever rock was present (26-100% infilled; Table 1). Snapshots with clean, (0-5% interstitial space infilling present), angular rock present were mapped as ‘present’ (Table 2-1). Snapshots where appropriate primary substrate existed (gravel, rubble, cobble), but which were not sediment free (interstitial space infilling of 6-25%), were mapped as ‘marginal’ (Table 2-1).

These areas are not necessarily providing needed habitat structure for successful spawning but may be adjacent to, or along the margin of such areas.

Once these values were mapped, polygons enclosing areas where suitable spawning substrate existed were constructed by enclosing all areas where at least three adjacent snapshots with suitable spawning substrate were documented.

Final parameterization of spawning habitat criteria at suspected sites

The third objective was to determine values of additional habitat features which occur within the polygons of suitable spawning substrate (Table 2-2). Slope, aspect, fetch, and water depth for these areas were derived from a high resolution (10-m-pixel cell size) digital elevation model (DEM) provided in (Morgan et al. 2003).

Slope was defined as the maximum rate of change between the elevation value for each 10-m cell and the elevation values for its eight neighboring cells, expressed as a percentage (ESRI 2006). Slope was calculated for each 10-m cell by using the DEM data and the slope tool provided in ArcGIS Spatial Analyst (ESRI 2006).

Aspect was defined as the direction of the slope, or the direction from each cell to its neighbor with the greatest change in elevation. Aspect values can range from -1 where no change in elevation exists to 0^{o} through 360^{o} equivalent to a compass bearing in the direction between that cell and the cell with the greatest change in elevation. Aspect for each cell was derived from the DEM data using the aspect tool ArcGIS Spatial Analyst (ESRI 2006).

Fetch length, a surrogate for wave energy (Rowan et al. 1992), was calculated using DEM data, ArcGIS (ESRI 2006), and an analysis script developed specifically for that purpose (Finlayson 2005). The script required input of primary wind direction, a binary map describing water (coded as ‘1’) and the surrounding land mass, including any islands (coded as ‘0’). With this information, fetch length was calculated as the average of distance to shore along nine wind radials: the primary wind direction, and another eight directions offset by consecutive 3^o increments: -12, -9, -6, -3, 3, 6, 9, and 12 from the primary wind direction (Coastal Engineering Research Center 1984). Direction of the prevailing winds during spawning season was used for this calculation (Brian Ertel and Philip Doepke, National Park Service, Yellowstone National Park, personal communication).

Geologic formation origin for each polygon was obtained by overlaying spawning habitat polygons with geologic origin data layers (Morgan et al. 2003) and noting the intersection of the two.

Distance to deep water or refuge was calculated for both the shortest distance to areas of at least 20 m and to at least 30 m in depth. Straight-line distance to the closest cell of at least 20 m and at least 30 m depth were measured for each cell within each polygon of suitable spawning substrate.

Two of the developed polygons defining the boundaries of the suitable spawning substrate were smaller than the resolution of most of the data layers (10 m). In order to include information from these polygons and to accommodate the irregular shape of all polygons, all raster data layers were re-sampled to a resolution of 1 m^2 for this analysis (Figure 2-13).

Values for depth slope, aspect, fetch, geology, and distance to refuge for each 1-m cell occurring within each polygon boundary were tabulated and summarized (mean, minimum, maximum, and standard deviation) for each polygon.

Results

Bottom substrate for 977 snapshots taken from 68 transects conducted at the suspected spawning areas were classified during the initial data review. A high percentage (78.8%) of these snapshots were classified as having both primary and secondary substrate consisting of sand, silt, or vegetation. At Carrington Island, the majority of actual rock (gravel, rubble, cobble, bedrock, or thermal substrate) seen consisted of rubble (Table 2-3). Areas which were considered ‘clean’, with no visible sediment, vegetation, or sand, were located primarily at either end of the island, but 3 small polygons were also spotted around the island (Figures 2-7 and 2-14).

The rock present in the area near West Thumb geyser basin was much more diverse, consisting of gravel, cobble, boulder, and thermal substrates (Table 2-3). However, observations of clean, angular substrate occurred in only two small polygons near the southern end of the examined area (Figures 2-9 and 2-15). These areas consisted almost entirely of rubble, with small amounts of gravel intermixed. Both polygons occurred along the edge of a submerged cliff face due a past thermal explosion (Morgan et al. 2003). Although the cliff face extended along a large part of the surveyed area, no other suitable substrates were seen.

Near Solution Creek, substrate was almost exclusively sand, silt, or vegetation (Table 2-3). Very little rocky substrate was observed; however what was seen was composed of either rubble or thermal substrate. No clean, rocky substrate was observed in this area (Figures 2-11 and 2-16). Therefore, no polygons from this area were used in the final parameterization of spawning habitat criteria.

Parameterization of spawning habitat criteria

Seven polygons denoting suitable spawning substrate (Table 2-4), five near Carrington Island (Figure 2-7) and two near the West Thumb geyser basin (Figure 2-9) were used to summarize values of habitat features for areas of suitable spawning substrate.

Mean, minimum, maximum, and standard deviation values are reported in Appendix B for depth, slope, and distances to 20 m depths, 30 m depths, thermal vents, and shore. Minimum and maximum only are reported for aspect as values of 0^{o} and 360^{o} are equal making mean and standard deviation meaningless. Fetch length was calculated with prevailing wind direction set at west-southwest (247^{o}).

Geologic classes for the lake bottom were lake sediments for Carrington Island polygons and hydrothermal explosion for the West Thumb geyser basin polygons (Morgan et al. 2003).

Discussion

Boundaries of known spawning sites

Lake trout spawning substrates of clean, angular rubble and cobble were identified at two of the three suspected spawning areas. Specifying a minimum size of constructed polygons eliminated a few areas at Carrington Island where suitable substrate occurred in very small pockets. Possibly lake trout use these areas for spawning; however, their small size (<10 m^2) is well below the resolution of the data sets used and so were excluded.

Direct observation of lake trout spawning has occurred at the two, shallow polygons just off Carrington Island while electrofishing the area (personal observation). Similarly, although electrofishing encircled the entire island, very few lake trout have been caught outside of the polygons designated as having suitable spawning substrate by this study (personal observation). Direct observations at the other three Carrington Island polygons have not been possible because water depths were greater than efficient affects of the electric current.

Polygons mapped with suitable spawning substrate at the West Thumb geyser basin area are well within locations where gravid lake trout are regularly observed in NPS gillnet catch data (Figure 2-3).

Given that no suitable spawning substrates were found at the Solution Creek area, this suggests that the area may be either a staging area or travel corridor to other spawning sites. Although NPS gillnet catch data indicate high catches of mature lake trout in these areas (Figure 2-3), it is possible no spawning occurs here. Typically during peak lake trout spawning, fairly precise placement of gillnets over small elevated areas in the lake floor is required here to yield the best catch rates of mature lake trout (Stacey M. S. Gunther and Philip D. Doepke, personal communication).

It is also possible that data collection intensity was not great enough to locate small patches of suitable substrate. If all suitable substrate at this site, or additional suitable substrate at the other two sites, occurred in patches small enough to fall completely between transects, they would have been missed. Further examination of this area, perhaps with divers who have a 360^{o} perspective, would be useful to determine whether or not the Solution Creek area is used by lake trout for spawning in Yellowstone Lake.

Final parameterization of spawning habitat criteria

Values for other habitat features found within the seven polygons delineating suitable substrate structure were well within those reported in the literature. Nevertheless, given that features of spawning habitat may have a strong correlation with depth and size of a given lake (Martin 1957), detailing this information for Yellowstone Lake is an important step in understanding lake trout spawning habitat available in Yellowstone Lake.

It was surprising to see that geologic origin of the Carrington Island sites were lake sediments according to Morgan et al (2003). This is in direct contrast to substrate classes found. Apparently, the resolution of this data layer is such that it is not appropriate for detecting small areas of suitable substrate for spawning.

The distances to waters of depths of both 20 and 30 m for the sites surveyed were well within easy travelling distance for lake trout, ranging from a mean of 20.0 m at a polygon near West Thumb geyser basin to 183.7 m at Carrington Island for 20-m water. Similarly, distance to 30-m water (ranging from 40.0 m to 244.2 m) is also easily traveled by lake trout.

Conclusions

Presence of suitable lake trout spawning substrate was found in two of the three suspected lake trout spawning areas. Values for depth, interstitial spacing, slope, and distance to deep-water refuge all appeared well within published norms for the species. Delineating and categorizing what is currently known to be important spawning habitat used within the lake is a valuable starting point for predicting future use in a lake-wide model described in the next chapter.

References

Beauchamp, D. A., B. C. Allen, R. C. Richards, W. A. Wurtsbaugh, and C. R. Goldman. 1992. Lake trout spawning in Lake Tahoe: egg incubation n deepwater macrophyte beds. North American Journal of Fisheries Management 12:442-449.

Biga, H., J. Janssen, and J. E. Marsden. 1998. Effect of substrate size on lake trout egg predation by mottled sculpin. Journal of Great Lakes Research 24:464-473.

Bigelow, P. E., and five coauthors. 2003. Protection of native Yellowstone cutthroat trout in Yellowstone Lake, Wyoming. Final Report. Technical Report NPS/NFWRD/NRTR-2003/314. 12 pages.

Coastal Engineering Research Center. 1984. Shore Protection Manual, volume I. U.S. Army Corps of Engineers, Waterways Experiment Station,Vicksburg, Mississippi.

DeRoche, S. E. 1969. Observations on the spawning habits and early life of lake trout. The Progressive Fish-Culturist 39:109-113.

Edsall, T. A., and G. W. Kennedy. 1995. Availability of lake trout reproductive habitat in the great lakes. Journal of Great Lakes Research 21(SUPPL. 1):290-301.

Edsall, T. A., P. T. P., N. R. T., and B. C. L. 1998. Side-Scan Sonar Mapping of Lake Trout Spawning Habitat in Northern Lake Michigan. North American Journal of Fisheries Management 9:269-279.

ESRI, I. 2006. ArcGIS, Redlands, California.

Finlayson, D. 2005An ArcGIS 9.0 toolbox with scripts designed to calculate fetch length, wave height and wave period for all water cells in a DEM. http://students.washington.edu/dfinlays/scripts/ (Accessed March 2005).

Fitzsimons, J. D. 1995. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. Journal of Great Lakes Research 21(SUPPL. 1):337-347.

Flavelle, L. S. 2003. A description of space use and habitat selection in Lake Opeongo lake trout *Salvelinus namaycush*. Master of Science thesis. University of Waterloo, Waterloo, Ontario, Canada.

Flavelle, L. S., M. S. Ridgway, T. A. Middel, and R. S. McKinley. 2002. Integration of acoustic telemetry and GIS to identify potential spawning areas for lake trout *Salvelinus namaycush*. Hydrobiologia 483:137-146.

Gunn, J. M. 1995. Spawning behavior of lake trout: Effects on colonization ability. Journal of Great Lakes Research 21(SUPPL. 1):323-329.

Gunn, J. M., M. Conlon, R. J. Kirk, and S. C. McAughey. 1996. Can trained observers accurately identify lake trout spawning habitat? Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):327-331.

Johnson, N. S., M. J. Siefkes, and W. Li. 2005. Capture of ovulating female sea lampreys in traps baited with spermiating male sea lampreys. North American Journal of Fisheries Management 25:67-72.

Kaeding, L. R., G. D. Boltz, and D. G. Carty. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries 21(3):16-20.

Kelso, J. R. M., W. R. MacCallum, and M. L. Thibodeau. 1995. Lake trout spawning at five sites in Ontario waters of Lake Superior. Journal of Great Lakes Research 21(SUPPL. 1):202-211.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative Lake Trout Result in Yellowstone Cutthroat Trout Decline and Impacts to Bears and Anglers. Fisheries 30(11):10-19.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2007. Yellowstone Fisheries and Aquatic Sciences Annual Report, 2006. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2007-04.

MacLean, N. G., and six coauthors. 1990. Environmental and genetic factors affecting the physiology and ecology of lake trout. Lake trout synthesis, Physiology and Ecology Working Group. Ontario Ministry of Natural Resources. Toronto.

Marsden, J. E., and nine coauthors. 1995. Lake trout spawning habitat in the Great Lakes - A review of current knowledge. Journal of Great Lakes Research 21(SUPPL. 1):487-497.

Martin, N. V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. Transactions of the American Fisheries Society 86:231-244.

Martin, N. V., and C. H. Olver. 1980. The lake charr. Pages 205-277 *in* E. K. Balon, editor Charrs: salmonid fishes of the genus Salvelinus. Kluwer Boston, Inc., Hingham, Massachusetts.

Morgan, L. A., and 13 coauthors. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 122:221-242.

Munro, A. R., T. E. McMahon, and J. R. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush)* in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Science 62:79-87.

Piper, R. G., I. B. McElwain, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. Fish Hatchery Management. United States Department of the Interior, Washington D.C.

Rowan, D. J., K. J., and R. J. B. 1992. Estimating the mud deposition boundary depth in lakes from wave theory. Canadian Journal of Fisheries and Aquatic Sciences 49:2490-2497.

Ruzycki, J. R. 2004. Impact of lake trout introductions on cutthroat trout of selected western lakes of the continental United States. PhD. Utah State University, Logan, Utah.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone lake. Ecological Applications 13:23-37.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada Bulletin 184(Lake Trout *Salvelinus namaycush* (Walbaum)):220-229.

Sly, P. G. 1988. Interstitial Water Quality of Lake Trout Spawning Habitat. Journal of Great Lakes Research 14:301-315.

Young, M. K. 2001. Pheremonal attraction: the potential for selective removal of nonnative species. Proceedings of Practical Approaches for Conserving Native Inland Fishes of the west. June 6-8, 2001, University of Montana, Missoula, Montana.

DEVELOPMENT OF A LAKE TROUT SPAWNING HABITAT MODEL USING ARCGIS CAPABILITIES

Lake trout *Salvelinus namaycush*, a recently introduced piscivore to Yellowstone Lake, pose a significant threat to Yellowstone cutthroat trout *Oncorhynchus clarki* in Yellowstone Lake (Koel et al. 2005). As such, the National Park Service has launched intensive removal efforts aimed at reducing this voracious predator. However, removal efforts are time consuming and, if directed inappropriately, may be ineffective. They can also be complicated by concurrent residency of the native, intended beneficiary of removal efforts. In the case of Yellowstone Lake, Yellowstone cutthroat trout often occupy areas of the lake where lake trout also reside (Benson 1961). Lake trout are typically a non-schooling species (Scott and Crossman 1973), making it difficult to capture large numbers at once.

Three attributes of lake trout spawning behavior make this aspect of their life history a vulnerable attack point for efficient removal efforts. First, they spawn in groups. Lake trout congregate over spawning areas for several days, with males staying longer than females (Martin and Olver 1980; Scott and Crossman 1973). This results in areas of high densities of adult lake trout vulnerable to removal efforts. Second, lake trout neither prepare the substrate on which the eggs are deposited nor provide any protection for their developing embryos, relying solely on the spawning site to provide adequate conditions. This, limits the areas which are suitable for lake trout spawning. Third, lake trout exhibit at least some homing to natal spawning areas. This would facilitate control efforts for an expanding population, such as is present in Yellowstone Lake, which has not fully capitalized on all spawning habitat that may be available in the lake. If spawning areas can be located and targeted for removal efforts, population expansion may be restricted.

The goal of this project was to identify areas with the highest potential to present suitable spawning habitat for lake trout in Yellowstone Lake. Specific objectives were to incorporate pertinent physical habitat data available for Yellowstone Lake with necessary spawning habitat in order to identify areas of potential lake trout spawning habitat and identify physical habitat features that have the strongest influence on model predictions.

Lake trout spawning habitat

Specific habitat structure is critical to the reproductive success of lake trout (Marsden et al. 1995). Basic functions such as access, shelter, and a supply of fresh water, must be provided to have suitable spawning habitat (Figure 3-1). Access to the area must be available for adults to immigrate and for juveniles to emigrate to nursery habitat as they mature (Marsden et al. 1995). Some evidence exists to suggest that lake trout congregate in staging areas in close proximity to spawning areas as spawning season approaches and during the spawning period (Scott and Crossman 1973). Characteristics of staging areas are unknown, but given lake trout are known to enter shallow water to spawn, it is safe to assume some minimum depth, possibly dictated either by light penetration or thermal limits, is required by lake trout when not spawning during daylight hours.

Selected habitat must also provide a substrate with shelter for developing embryos and fresh water for oxygenation and removal of developmental waste products (Sly 1988). Factors such as wave action, fetch, wind energy, substrate size, and interstitial spaces work in combination to provide habitat for developing embryos (Flavelle et al. 2002). Lake trout make no attempt to bury or guard their embryos after spawning (Martin and Olver 1980; Scott and Crossman 1973). Fertilized eggs are negatively buoyant and descend into interstitial spaces in the substrate. This behavior makes the choice of spawning site critical to the survival of the offspring.

Substrate sizes used by lake trout for spawning vary greatly. Scott and Crossman (1973) reported that lake trout spawning occurs most often over large boulder or rubble substrate. In the Great Lakes, Edsall and Kennedy (1995) examined five known spawning areas and found the best substrate for lake trout spawning at each site ranged from gravel (2-64 mm diameter) to fractured bedrock with loose rocks scattered on the surface.

Spawning depths also range widely. In small- to medium-sized inland lakes, depths tend to be shallow. Scott and Crossman (1973) reported spawning generally occurred at depths less than 12 m. Flavelle et al. (2002) observed mature lake trout in Lake Opeongo, Ontario using areas of 1.7-8.4 m depth during what were believed to be spawning activities. MacLean et al. (1990) indicated that spawning areas occurred most commonly in depths less than 4 m deep among lakes in Ontario. However, lake trout spawning has been reported to occur at depths as great as 55 m in the Great Lakes (Martin and Olver 1980) and at 40-60 m deep in Lake Tahoe (Beauchamp et al. 1992).

Interstitial spaces among substrate particles are another important attribute of spawning habitat (Sly 1988). Substrate must exhibit a high proportion of cracks and crevices to allow fertilized eggs to sink into interstitial spaces (MacLean et al. 1990; Marsden et al. 1995). Interstitial spaces are thought to provide protection from predators (Biga et al. 1998). They must also allow for adequate water flow for embryos to remain aerated and toxin free (Sly 1988).

Slope, another potentially important feature of lake trout spawning habitat, is not well documented. However, Fitzsimons et al. (2005) reported lake trout spawning in areas with slopes of $30\text{-}40^{o}$ in Keuka Lake, New York. In Lake Ontario, suitable lake trout spawning habitat has been documented in areas with slopes of $20\text{-}45^{o}$ (Fitzsimons 1995).

Fetch length (distance from land along a given wind direction) is important in creating wave intensity (Rowan et al. 1992). Maclean et al. (1990) report a minimum requirement of 0.5 km to provide suitable lake trout spawning habitat. Although maximum fetch length is rarely reported, (Fitzsimons 1995) found egg survival to the eyed stage was inversely related to wind fetch, Fetch length at their study sites in Lake Ontario ranged from <1-76 km.

Slope, substrate size, wind fetch, water temperature, prevailing wind direction, and dissolved oxygen are all important variables to lake trout when choosing a spawning site (MacLean et al. 1990). More importantly, the interaction of these variables creates suitable spawning and incubation conditions.

Rowan et al. (1992) theorized that by using wave energy and particle threshold dynamics, they could predict the boundary between low-energy, deposition zones with accumulated fine-grained cohesive sediments and high-energy, erosive zones with coarse-grained non-cohesive sediments. Low accumulation of sediments is likely an important attribute of lake trout spawning habitat (Gunn 1995).

Rowan et al's (1992) final equation, using fetch as the surrogate for maximum wave height is:

$$\text{Log DBD} = -0.107 + 0.742 * \log F + 0.0653 * S \text{ where,}$$

DBD = the deposition boundary depth between erosion and deposition (m),
F = fetch along the longest axis, and
S = slope (%).

Adapting Rowan et al.'s (1992) function, Flavelle et al. (2002) suggested lake trout take advantage of the areas developed by the dynamics of wave action, and choose sites with appropriately aerated and cleaned substrate. Flavelle et al. (2002) predicted spawning sites would occur within either the erosive zone or a transition area 1 m depth both sides of the estimated boundary, and termed this area the transition zone. They adapted the equation by using only weather data during lake trout spawning activity (in their case, October) to define fetch as maximum distance to shore along the prevailing wind direction. Locations of all known spawning sites in their study area, Lake Opeongo, were found within the lake's transition or erosive zones.

Methods

A Habitat Suitability Index (HSI) model was constructed using ArcGIS (ESRI 2006). Data for model development from Yellowstone Lake included bathymetry data developed from a Digital Elevation Model (DEM; Morgan et al. 2003) and wind direction. Model variables derived from these inputs included slope, fetch, transition/erosive zones, depth, distance to refuge where refuge is considered a minimum depth, and distance to thermal vents. Data layers were combined using map algebra to produce an initial spawning habitat map. This initial map was developed as a starting point for a sensitivity analysis. Values used to set the criteria for suitable habitat for this initial map were based on the published literature (Edsall et al. 1992; Edsall et al. 1995; Fitzsimons 1995; Gunn et al. 1996; Kelso et al. 1995; MacLean et al. 1990; Marsden et al. 1995; Sly 1988).

Slope was calculated as a percentage value from the DEM using ArcGIS Spatial Analyst (ESRI 2006). Using the raster calculator, slope less than or equal to 45% were considered acceptable and classified as 1; everything with slope greater than 45% was classified as 0. When map algebra is performed to combine all data layers, all areas where any data layer has a value of 0 will be excluded as unacceptable.

Fetch was calculated using prevailing wind direction and distance to shore, ArcGIS (ESRI 2006), Python 2.3 (Anonymous 2005), and a script specifically written to calculate fetch (Finlayson 2005). In order to run properly, a binary map was constructed having water representing Yellowstone Lake set to

0 and land set to 1. Prevailing wind direction was obtained from resident experts (Brian Ertel and Philip Doepke, National Park Service, Yellowstone National Park, personal communication) and entered as a parameter for the script. This fetch data layer was reclassified using fuzzy logic (Guertin et al. 2000). Areas where fetch was greater than 5 km were deemed unacceptable because of substrate instability and classified as 0. Fetch was considered to have no effect when less than 1.5 km and were coded with a one. A straight-line relation was used for all values in between by determining the linear equation that fits a straight slope between the x,y points with values representing the no effect of up to 1.5 km (1.5, 1) and unacceptable effect of 5 km (5.0, 0):

$$\text{Fuzzyfetch} = (-0.0029 * \text{Fetch247}) + 1.428571,$$

where, Fetch247 is equivalent to straight-line fetch (Finlayson 2005) with wind direction equal to 247°.

The transition/erosive zones were estimated by first calculating the boundary between erosive and deposition zones using the equation discussed earlier (Rowan et al. 1992). The transition zone was set as +/- 1 m depth of the boundary (Flavelle 2003) and the erosive zone was considered to be anywhere that depth was less than or equal to the boundary depth. A binary map of the areas within the erosive and transitional zones (value = 1) and those outside either of those zones (value = 0) was developed via Spatial Analyst (ESRI 2006).

Distance to refuge was calculated by determining Euclidean distance from each datum cell within Yellowstone Lake to the nearest cell of at least 30 m depth. For example, if at a given cell, depth is 32 m, distance to a depth of at least

30 m would be 0. If depth were 15 m, distance was determined to the closest cell with depth at least 30 m. The resultant map was reclassified, again using fuzzy logic (Guertin et al. 2000), with values less than 0.5 km considered insignificant (value = 0), greater than 1 km to be large enough to discourage travel to that particular cell of the lake, and a straight-line function between the two (x,y = 0.5, 1 and 1.0,0), by using the equation:

$$\text{FuzzyDistRefuge} = (-0.002 * \text{Dist30m}) + 2,$$

where, Dist30m equals Euclidean distance to a depth of at least 30 m.

Areas with depth greater than 40 m were excluded to eliminate areas not likely to be used by lake trout in Yellowstone Lake by creating a simple binary map. Areas where depth was greater than 40 m were reclassified as 0, areas equal to or shallower than 40 m were reclassified as 1.

The resultant HSI map was made by multiplying the slope, fuzzy fetch, transition/erosive zone, fuzzy distance to refuge, and depth maps together. The fuzzy values were reclassified into categories that ran from 0, 0-0.25, 0.25-0.50, 0.50-0.75, 0.75-1.0, as none, poor, fair, good and excellent potential spawning habitat.

Results

Values for data layer classifications and resultant percentage of the total area of Yellowstone Lake are reported in Table 1. Water depths greater than 40 m comprised 54.1% of Yellowstone Lake (Table 3-1; Figure 3-1). Areas with slopes less than or equal to 45^o comprised almost the entire lake (92.2%; Table 3-1;

Figure 3-2). The erosive/transition zones included 35.9% of the lake habitat (Table 3-1; Figure 3-3). Distance to a refuge of 30-m-deep waters included more than 99.9%of the lake (Table 3-1; Figure 3-4). Lastly, fetch included 66.3% of the lake, with 39.0% valued at ‘1’, leading to full inclusion for those cells in the fetch data layer (Table 3-1; Figure 3-5). When all data layers were combined, resultant values for potential lake trout spawning habitat were none for 88.1% of the lake area, poor for 2.1%, fair for 2.1%, good for 2.1%, and excellent for 5.7% of Yellowstone Lake (Table 3-1; Figure 3-6).

Discussion

Although excluding depths 40 m and greater eliminated 54% of the lake from further consideration as suitable spawning habitat (Table 3-1), this value is very liberal when compared to much of the published lake trout literature. Lake trout spawning has been documented at such depths in the Great Lakes and in Lake Tahoe (Beauchamp et al. 1992; Edsall and Kennedy 1995). However, by far the majority of lake trout spawning across their range occurs in water less than 10 m deep (MacLean et al. 1990; Martin and Olver 1980). In a lake the size of Yellowstone Lake, about five one-thousandths that of Lake Superior, we would not expect to see spawning in areas as deep because of the much reduced available fetch to create water movement in these deep areas (Martin and Olver 1980).

Very little information is reported in the literature on ranges of slope used by lake trout for spawning. We set our criteria for slope to be at the maximum reported (45^{o}; Fitzsimons 1995) in order to be inclusive of as much of the potential habitat as possible.

Acceptable fetch length was also set at liberal values to be inclusive of published data. Lake trout spawning has been reported in areas of fetch length up to 2.3 km (Fitzsimons 1995). However, generally, minimum fetch, not maximum is reported in the literature (Fitzsimons 1995). Although we did fuzzify this parameter, our fuzzy equation was based on a straight line relationship. It is likely, as demonstrated by Rowan et al. (1992) that the relationship is log-based. Future use of these data may benefit by incorporating a log-based relationship when developing a relationship between fetch length and spawning habitat suitability. Approximately 34% of the lake was excluded based on fetch alone.

Given the ranges of suitable substrate size, depth, and fetch, it seems very reasonable to expect a combination of these three variables to identify suitable spawning areas. However, calculating the erosive and transition zones did not eliminate much the lake. Slightly over 64% of the lake was outside of these areas and therefore theoretically not suitable for lake trout spawning. Undoubtedly in a lake as large as Yellowstone Lake, areas far into the erosive zone exhibit too much substrate movement and do not provide adequate protection for the developing eggs and embryos (Fitzsimons 1995). However, at this point data to set a limit are not available.

Although staging areas are often cited as being important to the spawning process, they did not appear to be a limiting factor in Yellowstone Lake. Setting refuge equal to 30 m depth, and calculating distance to these areas, even with our fuzzy equation, still left 97% of the lake within acceptable distance of deep water refuge.

With the parameter values used, the resultant model indicated distance to a 30-m depth refuge was the least important input, while the erosive/transition zones and fetch affected results the most. Lake trout spawning activity is reportedly high immediately following storm events within the spawning season (Martin and Olver 1980). Thus it is interesting to note that the two most important attributes of the model rely heavily on wind direction.

When all data layers were combined, the resultant spawning habitat model indicated 88.1% of Yellowstone Lake had no potential for lake trout spawning habitat, greatly reducing the area needed to be monitored for lake trout spawning activity in future years.

Although our final map, the minimum of all data layers combined, left over 5% of Yellowstone Lake as potentially excellent lake trout spawning habitat, this was an exercise in examining the effects of several parameters on habitat suitability. All variables and equations were set liberally and, given more data on the habitat needs of lake trout, will become more restrictive. More refinement in fuzzy relationships and in reclassifying results will also improve a future model. We expect that fuzzifying the transition/erosive zone will provide will provide more precise criterion for determining spawning habitat suitability. As constructed, the resultant model has eight points where data input and data processes can be varied for future sensitivity analysis and to further refine and test the model’s efficacy (Figure 3-7). Prevalent wind direction can be varied to influence both the erosive/transition zone and the acceptable fetch data layers. Other adjustments can be made to the processes of manipulating the data, such as varying acceptable slope or depth. New information, e.g. distance to nursery areas, can easily be included by adding in additional data layers as the data become available.

Finally, as presented the last process in this model (Figure 3-7), where all the information are combined to produce the resultant map (Figure 3-6), currently give equal weight to all data layers. Along with future sensitivity analysis, additional methods of combining data layers, for example, differential weighting for each layer need to be explored.

Conclusion

We developed a habitat suitability index to give insight to potential locations of suitable spawning habitat. Parameters used included slope, fetch, depth, wave energy, and distance to deep water refuge. The resultant model indicated that 5.7 % of Yellowstone Lake provided excellent potential for lake trout spawning habitat. Future refinements of this model based on additional data on the habitat needs of lake trout for spawning and sensitivity analysis will likely provide more precise estimates of the locations of suitable spawning habitat.

References

Anonymous. 2005. Python programming language. A dynamic object-oriented programming language. www.python.org.

Beauchamp, D. A., B. C. Allen, R. C. Richards, W. A. Wurtsbaugh, and C. R. Goldman. 1992. Lake trout spawning in Lake Tahoe: egg incubation n deepwater macrophyte beds. North American Journal of Fisheries Management 12:442-449.

Benson, N. G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Research Report 56:33.

Biga, H., J. Janssen, and J. E. Marsden. 1998. Effect of substrate size on lake trout egg predation by mottled sculpin. Journal of Great Lakes Research 24:464-473.

Edsall, T. A., C. L. Brown, G. W. Kennedy, and T. P. Poe. 1992. Lake Trout Spawning Habitat in the Six Fathom Bank-Yankee Reef Lake Trout Sanctuary Lake Huron. Journal of Great Lakes Research 18:70-90.

Edsall, T. A., M. E. Holey, B. A. Manny, and G. W. Kennedy. 1995. An evaluation of lake trout reproductive habitat on Clay Banks Reef, Northwestern Lake Michigan. Journal of Great Lakes Research 21(SUPPL. 1):419-432.

Edsall, T. A., and G. W. Kennedy. 1995. Availability of lake trout reproductive habitat in the great lakes. Journal of Great Lakes Research 21(SUPPL. 1):290-301.

ESRI, I. 2006. ArcGIS, Redlands, California.

Finlayson, D. 2005An ArcGIS 9.0 toolbox with scripts designed to calculate fetch length, wave height and wave period for all water cells in a DEM. http://students.washington.edu/dfinlays/scripts/ (Accessed March 2005).

Fitzsimons, J., and seven coauthors. 2005. Deepwater spawning by lake trout (Salvelinus namaycush) in Keuka Lake, New York. Journal of Great Lakes Research 31:1-10.

Fitzsimons, J. D. 1995. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. Journal of Great Lakes Research 21(SUPPL. 1):337-347.

Flavelle, L. S. 2003. A description of space use and habitat selection in Lake Opeongo lake trout *Salvelinus namaycush*. Master of Science thesis. University of Waterloo, Waterloo, Ontario, Canada.

Flavelle, L. S., M. S. Ridgway, T. A. Middel, and R. S. McKinley. 2002. Integration of acoustic telemetry and GIS to identify potential spawning areas for lake trout *Salvelinus namaycush*. Hydrobiologia 483:137-146.

Guertin, D. P., R. H. Fiedler, S. N. Miller, and D. C. Goodrich. 2000. Fuzzy logic for watershed management. M. Flug, D. Frevert, and D. W. J. Watkins, editors. Proceedings of the ASCE Conference on Science and Technology for the New Millennium: Watershed Management 2000, Fort Collins, Colorado.

Gunn, J. M. 1995. Spawning behavior of lake trout: Effects on colonization ability. Journal of Great Lakes Research 21(SUPPL. 1):323-329.

Gunn, J. M., M. Conlon, R. J. Kirk, and S. C. McAughey. 1996. Can trained observers accurately identify lake trout spawning habitat? Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):327-331.

Kelso, J. R. M., W. R. MacCallum, and M. L. Thibodeau. 1995. Lake trout spawning at five sites in Ontario waters of Lake Superior. Journal of Great Lakes Research 21(SUPPL. 1):202-211.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative Lake Trout Result in Yellowstone Cutthroat Trout Decline and Impacts to Bears and Anglers. Fisheries 30(11):10-19.

MacLean, N. G., and six coauthors. 1990. Environmental and genetic factors affecting the physiology and ecology of lake trout. Lake trout synthesis, Physiology and Ecology Working Group. Ontario Ministry of Natural Resources. Toronto.

Marsden, J. E., and 13 coauthors. 1995. Lake trout spawning habitat in the Great Lakes - A review of current knowledge. Journal of Great Lakes Research 21(SUPPL. 1):487-497.

Martin, N. V., and C. H. Olver. 1980. The lake charr. Pages 205-277 *in* E. K. Balon, editor Charrs: salmonid fishes of the genus Salvelinus. Kluwer Boston, Inc., Hingham, Massachusetts.

Morgan, L. A., and 13 coauthors. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 122:221-242.

Rowan, D. J., K. J., and R. J. B. 1992. Estimating the mud deposition boundary depth in lakes from wave theory. Canadian Journal of Fisheries and Aquatic Sciences 49:2490-2497.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada Bulletin 184:220-229.

Sly, P. G. 1988. Interstitial Water Quality of Lake Trout Spawning Habitat. Journal of Great Lakes Research 14:301-315.

APPENDIX A

USE OF A SIMPLE UNDERWATER VIDEO SYSTEM COMBINED WITH GPS AND GIS TO MAP UNDERWATER SPAWNING HABITAT IN A LACUSTRINE ENVIRONMENT

Quantifying or even delineating specific fish habitat, especially in deep water, is often problematic for fisheries professionals. A detailed knowledge of habitat requirements and availability is critical to the understanding and proper management of any species. However, this often presents difficulties because of our inability to directly observe important attributes of a given habitat (e.g. substrate composition at spawning areas for a deepwater-spawning species). Access to specific habitat features of interest is often difficult and frequently requires extremely specialized training. Efforts to mitigate for these limitations have included the use SCUBA, aerial flights in situations where water clarity allows a birds' eye view to gain better perspective, and underwater video and still cameras configured with a variety of deployment methods.

SCUBA, often used for direct observation in aquatic work, requires extensive training for biologists involved and is often not worth the investment for small projects. For example, if working in a national park, participants are required to work in at least pairs, have additional surface support (dive tenders and diving platform), be SCUBA certified (e.g. NAUI or PADI), and be National Park Service (NPS) certified (e.g. must have successfully completed testing by an NPS dive master plus complete at least 10 dives and 40 hours of additional training annually). Further complications of working in a cold, high-altitude environment such as Yellowstone Lake require that divers be both dry-suit and high altitude certified as well.

When direct observation via snorkeling or SCUBA is prohibitive, a desirable option is indirect observation via use of photographic equipment. Examples discussed in the literature include heavily weighted cameras, cameras attached to Remotely Operated Vehicles (ROV), or permanently mounted cameras, such as to a dock or piling. In the Snake and Sacramento rivers, where strong river currents exist, heavily weighted (up to 32 kg) cameras, deployed from a boat-mounted davit, have been used to quantify fall chinook salmon (*Oncorhyncus tshawytscha*) spawning habitat (Dauble et al. 1999; Gard and Ballard 2003; Groves and Garcia 1998). In deep-water areas of the Great Lakes, an underwater camera, mounted to an ROV has been successfully used to map potential lake trout spawning habitat (Edsall et al. 1992; Edsall et al. 1995; Edsall et al. 1996). Fixed-position cameras, such as dock- or piling-mounted, are useful in monitoring a preset location such as a fish passage point (Faurot et al. 2000), but are rarely practical for evaluating or monitoring habitat.

While heavy weights, used in high velocity waters, were important for maintaining camera position relative to the operating vessel for mapping purposes, they are not necessary in the lacustrine environment and the additional drag made it more difficult to keep the camera assembly positioned directly under the boat. The ROV-mounted camera setup gives operators a great deal of control and maneuverability, making this an extremely versatile platform for camera deployment (Klump et al. 1995). However, the complexity and expense of use of an ROV also make it logistic- and cost-prohibitive for many uses.

In order to survey bottom substrate in calm, lake water, a simpler and less expensive approach was needed. A methodology with the ability to record substrate bottom in depths up to 60 m while simultaneously recording position and depth of the camera was needed. Additionally, portability and the ability to accurately measure size of objects in the field of view were considered necessary. Hence, we set up a simple underwater video system that would allow simultaneous recording of the camera view, depth, and location with the ability to accurately measure objects within the field of view of the camera (Figure A-1). The objective of this paper is to describe this system, problems encountered, modifications made, and recommendations for future use.

Methods

General description of the underwater video setup.–Basic components of this system include an underwater video camera, lasers and software to enable measurements, underwater light, towed sled (Figure A-1), control box, portable power source, and a recording system (Figure A-2). Additional components that enabled digitization of videography and data annotation of depth, date, surface water temperature, location, and user-annotated text (e.g. transect name) include a laptop computer, data annotator, video digitizer, and modified software. For water depth, surface water temperature, and GPS location, the boat’s on-board

GPS/sonar unit was cabled to communicate with the laptop computer. In this case, it was a Lowrance XCT-M15 unit.

Towed sled.–Deployment of the camera, lasers, and light required construction of a carrier that allowed for adjustment of camera and laser angles, was lightweight for easy handling, somewhat streamlined for towing, and provided protection for the camera, lasers, and lights in the event that the system accidentally collided with or became entangled on underwater substrate features. Using primarily Speed-Rail components, we designed and constructed a frame that met these requirements. All construction materials, with the exception of the camera, laser, and light mounts, are readily available parts (Table 3-1). The camera, laser, and light mounts were precision-tooled expressly for this application. The angles for all mounts can be adjusted 360^o in a ventral-dorsal plain, depending on specific needs. The U-bolt, used as an anchor point for the towing cable, can be adjusted forward or backward to control the angle the sled is towed at. The width of the laser mounts can be adjusted from xx cm to xx cm, also dependent on the specific need. Throughout this project, the lasers were set at a distance of 14 cm from each other with the camera located dead center. All were set at a 45^o viewing angle (Groves and Garcia 1998). Rails, which can hold additional weight, are mounted on each side of the sled near the bottom.

Underwater camera, lasers, and light.–The camera used was a miniature color underwater TV camera with a titanium pressure housing, 2.9 mm fixed focus (15.2 cm to infinity), wide angle lens (model Aurora purchased from Insite Pacific Inc., Solana Beach, CA). Red light lasers were used to enable measurements on video frames. By setting lasers parallel to each other a known distance apart along either side of the camera, the image produced in the video frame could be used as a size reference for all other items in the video frame. Lasers, along with software for extracting video frames (i.e. snapshots from the video stream), and making measurements within the video frame were obtained from C-Map Systems, Inc., Red Lodge, MT. A 250-watt halogen underwater light with 1,000-m aluminum housing (Multi Sea Light model ML1040) was added for work when daylight was insufficient for viewing. Typically, lighting was not necessary in water depths less than 20 m during daylight hours.

Cable, control box, and portable power source.–A cable, able to bring power to the camera, lasers, and light, return the video images to the surface, and be durable enough to withstand the rigors of working, and being hauled up down in deep (40 to 60 m) water environments, was custom built (Falmat Custom Cable Technologies, San Marcos, CA). Length of 100 m was chosen to encompass any area within Yellowstone Lake that might need to be filmed. The cable consisted of coaxial cable to return the video image to surface, surrounded by power cables for the camera, the two lasers, and two lights. A Kevlar braid ensheathed this to add extra strength and the entire thing was coated with “neon green polyurethane” (which is actually purple in color) for added protection and to improve handling (Figure A-3). This cable ran from camera, lasers, and light attached to the towed sled to a control box located at the surface (generally onboard a boat).

The control box provided power supplies, fuses, on/off switching capabilities, and indicator lights for the camera, lasers, and underwater light as well as a dimmer dial for the underwater light housed in a splash proof carrying case. This box could be directly plugged into an AC power source to provide the power needed for the system.

Typically power was provided by a portable generator, either a Honda EU1000 or EU2000, but a standard wall outlet was also used for testing the system prior to travelling to the field.

Recording system.–Recording the video stream was necessary to provide an archivable record of the substrate encountered and to allow later data analysis. A standard BNC connector, located in the control box, could be wired to any video recording device using standard coaxial cable. Hence the recording system could be as simple as a hand held camcorder or a VHS video recorder. However, because I also wanted to add information as text overlay on the video image, I choose to use a more complicated system consisting of a laptop computer, a video digitizer, and a data annotator with accompanying software (digitizer, annotator, and software was provided by C-Map Systems, Inc.).

The laptop computer used was standard equipment with typical graphics handling capabilities. The data annotator retrieved data from software running on the computer, overlaid that data as text on the analog video image, and sent it forward to the video digitizer. The video digitizer converted the analog video data, with the overlain text data, into digital video data files and recorded them to the laptop computer hard drive.

Additional data collected.–The data retrieved from the computer and entered as overlay on the video image consisted of date, time, GPS location (UTM, NAD 1983, Zone 12N), surface water temperature, water depth, and user-entered text such as transect name. Date and time were retrieved from the computer internal clock. GPS location, surface water temperature, and water depth were obtained from the on-board GPS/sonar unit. User text was entered into the software. All of these options could be turned on and off at any time during filming.

Deployment and filming.–Kevlar lining of the power/video cable insured the cable was also strong enough to use as the main deployment cable. So as not to add stress to cable connectors (to camera, lasers, and light) when lowering and raising the apparatus, a grip was used to attach the cable directly to the tow sled (Figure A-4). When working in deep water (greater than 20 m), a deck-mounted hand-crank winch was also attached to the U-bolt and used to raise and lower the apparatus (Figure A-4). This greatly improved the ease of handling.

To record data along pre-determined transects, the equipped towed sled was deployed from the deck of a small (22-foot) boat powered by an outboard motor. Angle of attachment and weighting on the towed sled was adjusted to allow it to travel upright and level through the water when towed at slow speeds. The apparatus was lowered into the water until laser dots were clearly visible in the field of view on the lake floor. Height above the lake floor was adjusted via the cable as the apparatus was towed along the transect, typically at 1 to 2 m above the substrate. Generally the light was used only in depths 20 m or greater and was set at 60% power to obtain the best image. Daylight in shallower depths was sufficient for clear images.

Where transects ran from deep water into shallow water, filming and recording continued until the camera emerged from the water, typically about 0.5 m.

Data extraction

The customized software used allowed, data extraction from the recorded video by taking ‘snapshots’, a single video frame, from the video stream. Data extraction was then accomplished by first calibrating the image in each snapshot by setting the known distance between laser points as a reference. Actual size of any object in the image could then be measured and recorded. Additional data, recorded on the image by the data annotator, could also be extracted from the snapshot image. As noted earlier, this typically included date, time, water depth, surface water temperature, GPS location, and transect name (designated by the user).

Results and Discussion

Once footage is post-processed (i.e. snapshots and pertinent data is extracted from the video stream), the data can easily be incorporated to a Geographic Information System using the recorded UTM data. Sampling area and information obtained can be mapped and polygons constituting appropriate data values for the habitat feature of interest can easily be added. For example, by displaying information collected along transects through a known spawning area and using a classification of excellent, marginal, or no rocky substrate, polygons encompassing dense areas snapshots of excellent substrate can be added to delineate potential spawning habitat (Figure A-5).

Difficulties encountered

We encountered three major difficulties with employing this method of data collection: (1) cable handling, (2) boat speed and subsequent tracking of the towed sled along the designated transect, and (3) laser visibility in shallow water. Several other minor difficulties also arose.

The design of our power/video cable was such that it provided power to the light, lasers, and camera, provided video transport back to the surface, and provided enough strength to be used as the sole method of deployment all within one cable. Consequently, it was heavier and harder to handle than would be a typical coaxial cable. Originally the thought was to have it be strong enough to negate the need for an additional cable used for actual deployment, towing, and retrieval. Because the cable was custom designed and specially made, we wanted its length to be inclusive of any potential uses in Yellowstone Lake. Both of these attributes, added stoutness and length, complicated handling procedures. It was not possible, because the cable became very slippery when wet, to effectively use this cable as the main source of deployment when working at depths greater than about 20 m. Use of the deck-mounted winch and cable became necessary and negated the need for the added strength. Although the added length was kept coiled in a tub when not in use, it added a great deal of weight and bulk to the entire setup and was also not necessary.

In order for the underwater camera to capture footage in focus, in was necessary for the apparatus to move at very slow speeds, much slower than the forward idle speed on the outboard motor used. Initial attempts to keep the footage focused and the apparatus tracking along designated transects involved continued shifting back and forth between forward-idle and idle. This worked well enough in shallow water where only several meters of cable were needed to keep the camera close to the substrate surface. However, in deep waters there was a strong tendency for the towed sled to start oscillating forward and backward caused by the shifting. This problem was eliminated by adding a trolling plate to the outboard motor.

In order to calibrate measurements from an extracted snapshot, it is important for the red dots produced by the parallel lasers to be visible in the view frame. On bright, sunny days in shallow water (less than 2 m), this was often not the case. We compensated for this problem by two methods. First, the width of the field of view when the sled was set directly on the bottom when the lasers were visible (for calibration) was measured. Subsequently, by setting the towed sled directly on the bottom in areas of interest, the width of the snapshot, instead of distance between lasers, was used for the calibration. The second approach, used when general estimates sufficed and the lasers had recently been visible, was to judge based on changes in the video stream relative to objects of interest.

Other minor, but annoying, difficulties encountered were glare on the computer screen and a time delay in the video image displayed on the computer screen. Using the given boat and deck-mounted winch, it was necessary to have the laptop situated in the open part of the boat. Often glare from the sun made it difficult if not impossible to clearly view the image displayed. Shade for the computer greatly improved visibility and had the added benefit of keeping the computer cooler on sunny days. It was difficult for both the person controlling camera height from the lake bottom and the person operating the boat to both view the computer screen. Also, because the video image was being digitized and then recorded, the computer display had a 1 to 2 second delay. In order for the boat operator to have a real time image of the bottom, a small tv monitor was added in-line to our setup (Figure A-6). This did not change processing time or reliability but did greatly improve the boat operator's response time to upcoming obstacles.

Management Applications and Conclusion

Use of an underwater camera mounted on a towed sled, such as this, provides a versatile tool for viewing habitat or conducting searches in areas otherwise difficult for researchers or managers to access. It also allows permanent documentation of features of interest. In this case, we were able to view, record, and measure features at depths over 50 m in an inhospitable environment (high altitude, cold water temperatures, and occasional active thermal features such as underwater geysers and vents). When used for applications where added light or actual measurements are not needed, these components can be removed with no problems to the system. This setup is also quite portable and could be used in a variety of situations, for example, towed at depths limited only by the cable length, or suspended from a permanent structure, such as a bridge, to observe and record fish abundance or behavior rather than habitat features. In a situation where protection from collision with habitat or other underwater features is not an issue, the sled size can easily be reduced by removing and rearranging the Speed-O-Rail components, thus making it more adaptable to small, stationary spaces, such as a point for fish passage or trapping facility.

References

Dauble, D. D., R. L. Johnson, and A. P. Garcia. 1999. Fall chinook salmon spawning in the tailraces of lower Snake River hydroelectric projects. Transactions of the American Fisheries Society 128:672-679.

Edsall, T. A., C. L. Brown, G. W. Kennedy, and T. P. Poe. 1992. Lake Trout Spawning Habitat in the Six Fathom Bank-Yankee Reef Lake Trout Sanctuary Lake Huron. Journal of Great Lakes Research 18:70-90.

Edsall, T. A., M. E. Holey, B. A. Manny, and G. W. Kennedy. 1995. An evaluation of lake trout reproductive habitat on Clay Banks Reef, Northwestern Lake Michigan. Journal of Great Lakes Research 21(SUPPL. 1):419-432.

Edsall, T. A., G. W. Kennedy, and W. H. Horns. 1996. Potential spawning habitat for Lake Trout on Julian's Reef, Lake Michigan. Journal of Great Lakes Research 22:83-88.

Faurot, D., P. Kucera, and J. Hesse. 2000. Escapement monitoring of adult chinook salmon in the Secesh River and Lake Creek, Idaho. Bonneville Power Administration.

Gard, M., and E. Ballard. 2003. Applications of New Technologies to Instream Flow Studies in Large Rivers. North American Journal of Fisheries Management 23:1114-1125.

Groves, P. A., and A. P. Garcia. 1998. Two Carriers Used to Suspend an Underwater Video Camera from a boat. North American Journal of Fisheries Management 18:1004-1007.

Klump, V., and eight coauthors. 1995. 20,000 leagues under Yellowstone Lake, strangeness and beauty in the hidden deeps. Yellowstone Science 3(4):10-14.

Table 2-1. Classification scheme of site potential based on the presence of presence of rubble, cobble, boulders, bedrock, or thermal structures and amount of interstitial space infilling.

Substrate Class		Interstitial Spacing		
Primary	Secondary	0-5%	6-25%	26-100%; NA
Gravel, Rubble, Cobble, Boulder, Bedrock, or Thermal	Gravel, Rubble, Cobble, Boulder, Bedrock, or Thermal	present	marginal	none
Gravel, Rubble, Cobble, Boulder, Bedrock, or Thermal	Silt, Sand, or Vegetation	marginal	none	none
Silt, Sand, or Vegetation	Gravel, Rubble, Cobble, Boulder, Bedrock, or Thermal	none	none	none
Silt, Sand, or Vegetation	Silt, Sand, or Vegetation	none	none	none

Table 2-2. Parameters calculated for polygons of suitable lake trout spawning substrate at suspected lake trout spawning areas in Yellowstone Lake, Yellowstone National Park, Wyoming.

Parameter	Spatial data/ Source	Software used
Substrate class	Measured in field	VideoRuler
Interstitial spacing	Estimated in field	VideoRuler
Slope	Digital Elevation Model	Spatial Analyst, ArcGIS
Aspect	Digital Elevation Model	Spatial Analyst, ArcGIS
Fetch length	Digital Elevation Model	Fetch script, ArcGIS
Geology	USGS map	ArcGIS
Distance to refuge	Digital Elevation Model	Spatial Analyst, ArcGIS
Distance to thermal vents	USGS Map	Spatial Analyst, ArcGIS

Table 2-3. Substrate found at snapshots taken at three known spawning areas in Yellowstone Lake, Wyoming, using underwater videography.

Site	Carrington Island	WT geyser basin	Solution Creek	Total
Boulder/Bedrock	0	16	2	18
Cobble	2	9	0	11
Rubble	41	34	16	91
Gravel	15	9	9	33
Thermal	0	12	42	54
Sand/Silt/Vegetation	59	307	404	770
Total	117	387	473	977

Table 2-4. Habitat polygons developed for each spawning area.

Spawning area	Polygon ID	Area (m^2)
Carrington Island	0	115.1
	1	292.2
	2	664.6
	3	107.6
	4	82.7
WT geyser basin	5	68.4
	6	23.1

Table 3-1. Percent of Yellowstone Lake, Wyoming for each of several constructed data layers: depth, slope, erosive/transition zones, distance to refuge, and fetch and results from a recombination of these layers to form an initial Habitat Suitability Index model.

Map	Classification	% of Yellowstone Lake
Depth less than or equal to 40 m	0	54.14%
	1	45.86%
Slope less than or equal to 45 degrees	0	7.82%
	1	92.18%
Erosive/Transition Zones	0	64.06%
	1	35.11%
Fuzzy Distance to 30 m Refuge	0	0.86%
	1	0.45%
	2	0.74%
	3	1.18%
	4	96.78%
Fuzzy Fetch, using wind direction of 247 degrees	0	33.71%
	1	6.83%
	2	8.76%
	3	10.91%
	4	38.96%
Initial Habitat Suitability Index Model classifications.	unsuitable	88.1%
	poor	2.05%
	fair	2.13%
	good	2.07%
	excellent	5.65%

Table A-1. Parts used in construction of tow sled.

Item	Cost	Quantity	Total
Camera/Laser Mount Bracket	$ 240.00	1	$ 240.00
Camera/Laser Mount Base	$ 215.00	1	$ 215.00
Laser Mount	$ 110.00	2	$ 220.00
Lift Bail Shackles	$ 4.00	2	$ 8.00
Aluminum Structural Fittings	$ 6.58	30	$ 197.40
Aluminum Structural Fittings	$ 6.62	10	$ 66.20
Aluminum Structural Fittings	$ 10.26	2	$ 20.52
Aluminum Structural Fittings			
Shipping	$ 28.90	1	$ 28.90
3/4" Aluminum IPS Pipe	$ 90.63	20 ft	$ 90.63
Miscellaneous Hardware	$ 14.46	1	$ 14.46
Total			$ 1,101.11

APPENDIX B

Appendix B. Attributes of polygons of spawning habitat at three suspected spawning areas in Yellowstone Lake, Wyoming, including mean, minimum, maximum, and standard deviation (SD) for each polygon of lake trout spawning habitat. (CI = Carrington Island and WT = West Thumb geyser basin areas.)

Attribute	Area	ID	Count 1-m^2 cells	Mean	Minimum	Maximum	SD
Depth (m)	CI	0	114	3.05	3.0	3.0	0.000
		1	292	2.63	0.6	3.0	0.466
		2	683	3.63	2.4	4.0	0.216
		3	104	3.05	3.0	3.6	0.043
		4	85	2.17	2.1	3.0	0.169
	WT	5	71	13.07	11.9	14.6	1.250
		6	23	13.72	13.7	13.7	0.000
Fetch (m)	CI	0	114	174.1	135.6	218.9	39.36
		1	292	257.6	247.8	272.2	5.71
		2	683	277.31	251.1	313.3	15.96
		3	104	326.0	224.4	348.9	19.51
		4	85	275.0	137.8	284.4	17.48
	WT	5	71	304.3	295.6	311.1	5.11
		6	23	302.2	302.2	302.2	0.00
Aspect (degrees)	CI	0	114	-	-1.0	315.0	-
		1	292	-	67.8	156.8	-
		2	683	-	135.0	236.3	-
		3	104	-	-1.0	333.4	-
		4	85	-	18.4	341.6	-
	WT	5	71	-	273.1	285.7	-
		6	23	-	256.8	256.8	-
Slope (percent)	CI	0	114	1.54	0.0	5.3	2.03
		1	292	24.83	9.5	49.5	11.82
		2	683	9.89	5.0	36.1	7.38
		3	104	5.17	0.0	5.6	1.21
		4	85	35.58	11.9	36.4	4.54
	WT	5	71	77.07	68.9	89.0	7.71
		6	23	87.32	87.3	87.3	0.00

Appendix B (continued). Attributes of polygons of spawning habitat at three suspected spawning areas in Yellowstone Lake, Wyoming, including mean, minimum, maximum, and standard deviation (SD) for each polygon of lake trout spawning habitat. (CI = Carrington Island and WT = West Thumb geyser basin areas.)

Attribute	Area	ID	Count 1-m cells	Mean	Minimum	Maximum	SD
Distance to 20m-depths (m)	CI	0	114	132.9	130	140	4.43
		1	292	183.7	171	192	4.69
		2	683	176.4	139	206	16.81
		3	104	143.4	133	151	2.13
		4	85	164.4	160	170	4.93
	WT	5	71	26.9	20	32	4.99
		6	23	20.0	20	20	0.00
Distance to 30m-depths (m)	CI	0	114	188.6	184	196	4.56
		1	292	244.2	231	253	5.09
		2	683	242.76	206	273	16.83
		3	104	192.4	181	202	3.90
		4	85	220.3	214	226	4.84
	WT	5	71	53.2	45	58	5.18
		6	23	40.0	40	40	0.00
Distance to vents (m)	CI	0	114	543.1	535	546	4.29
		1	292	595.5	587	608	4.97
		2	683	586.3	553	611	17.26
		3	104	547.4	542	553	5.04
		4	85	574.3	564	585	5.81
	WT	5	71	40.5	30	41	2.05
		6	23	37.9	36	45	3.57
Distance to shore (m)	CI	0	114	36.2	28	42	4.78
		1	292	24.9	10	32	5.12
		2	683	46.7	28	67	9.04
		3	104	52.8	41	58	2.97
		4	85	21.42	20	32	2.18
	WT	5	71	267.1	260	273	4.51
		6	23	262.5	262	262	0.00

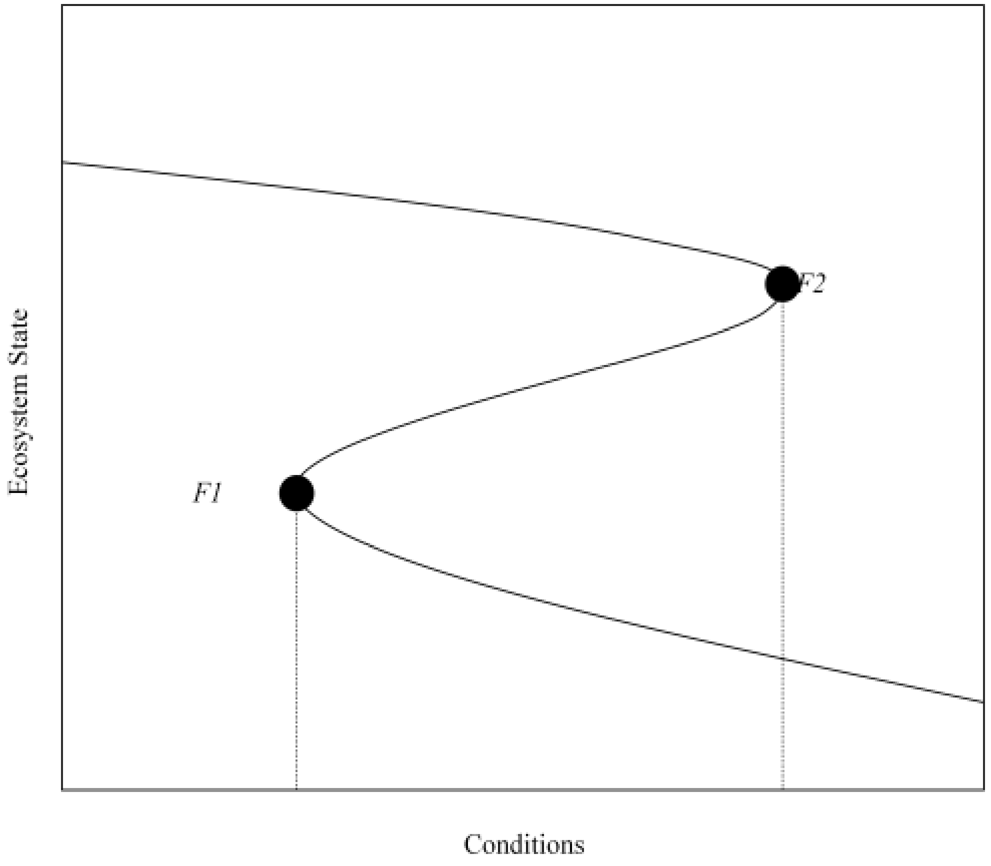

Figure 1-1. Ecosystem shift diagram showing hysteresis effect. The ecosystem can exist in the upper stable state, withstanding a large increase in conditions (F2) before any change is felt. However, once the state has been shifted to the lower stable state, conditions must decrease well below the level of F2 to F1 before the original stable state can be regained, if it can be regained at all (Scheffer et al. 2001).

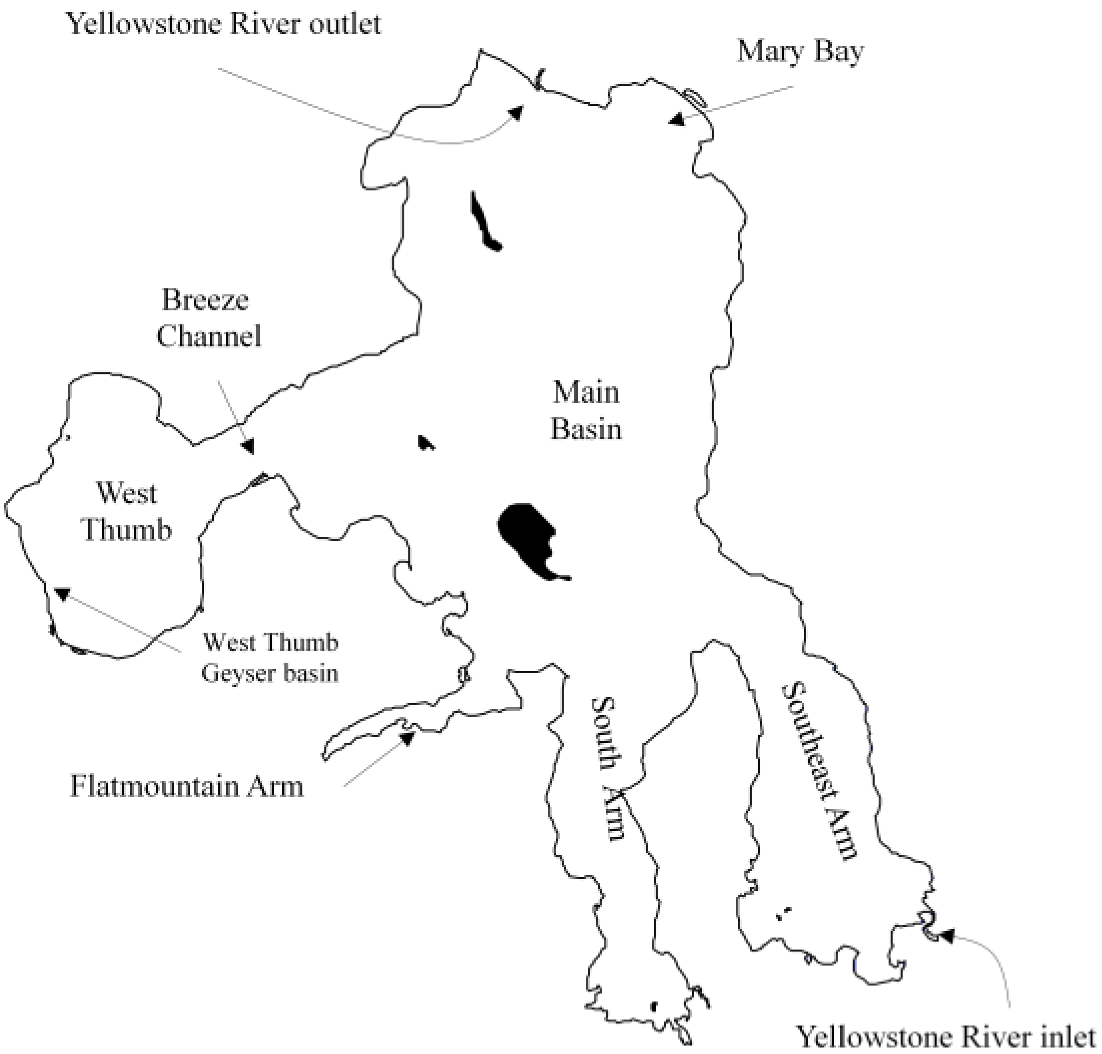

Figure 1-2. Yellowstone Lake, located in Yellowstone National Park, Wyoming, has one main basin (which extends into the Southeast Arm and 6 subbasins: West Thumb, the channel connecting West Thumb to the main basin called Breeze Channel, South Arm, Mary Bay, and one unnamed subbasin in the northern part of the lake just south of the Yellowstone River outlet.

Figure 1-3. Example of an anastomosing tubular structure from the floor of Yellowstone Lake, 2004. These features are found associated with active and inactive thermal vent fields throughout the lake.

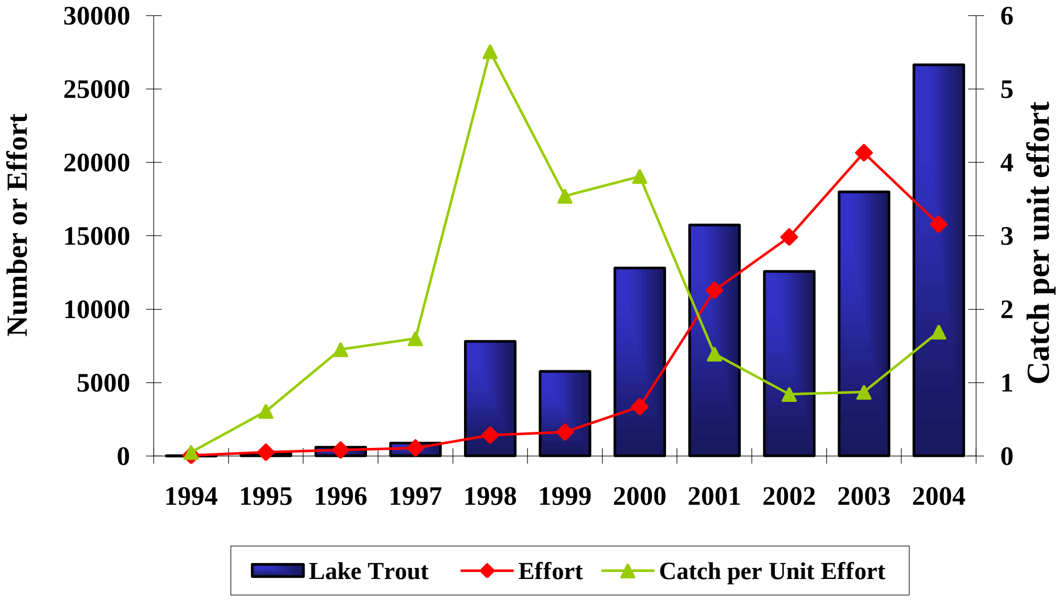

Figure 1-4. Number, effort (in 100 m of gillnet set 1 night), and catch per unit effort for lake trout removed from Yellowstone Lake, Yellowstone National Park, Wyoming, 1994 through 2004.

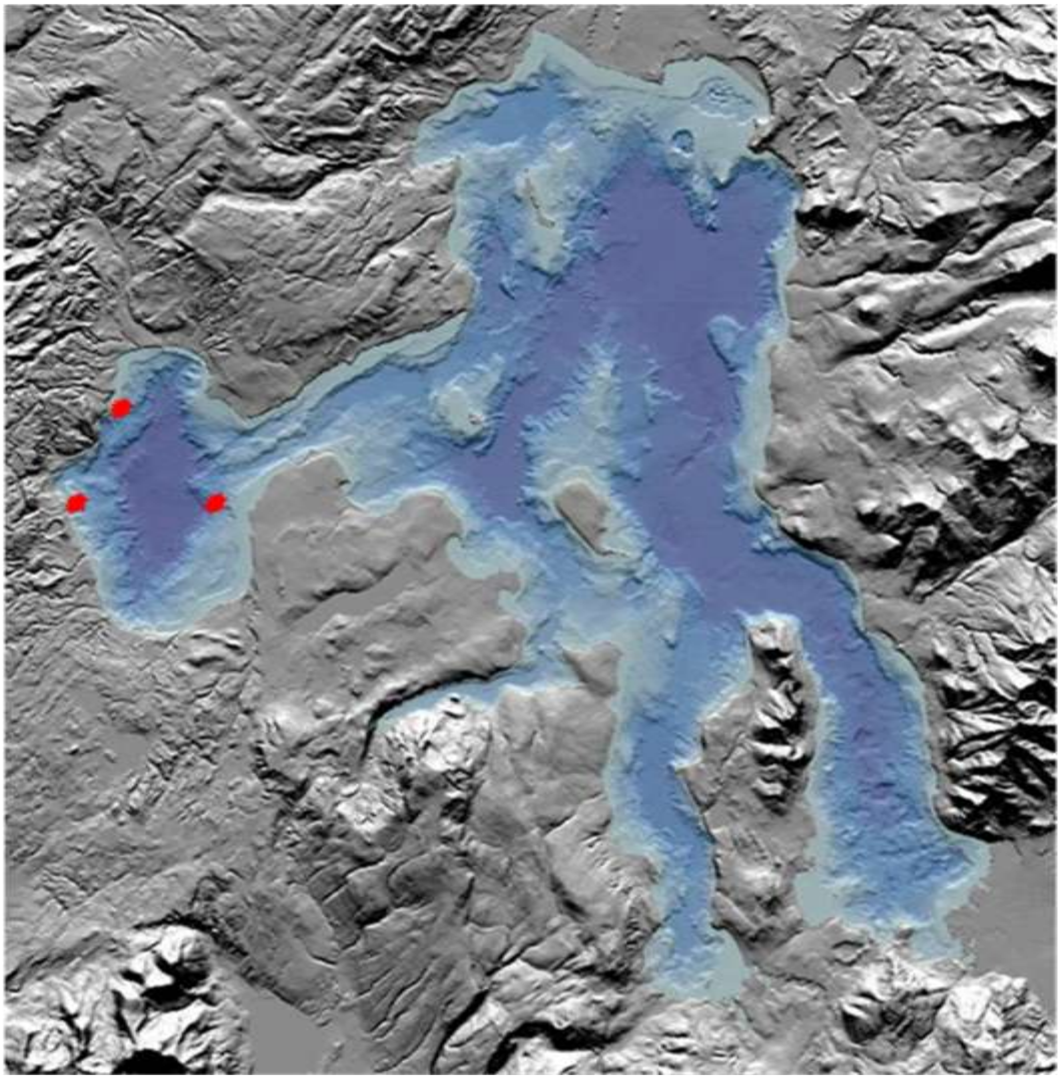

Figure 1-5. Yellowstone Lake, Wyoming, with suspected lake trout spawning areas marked by a red asterisk.

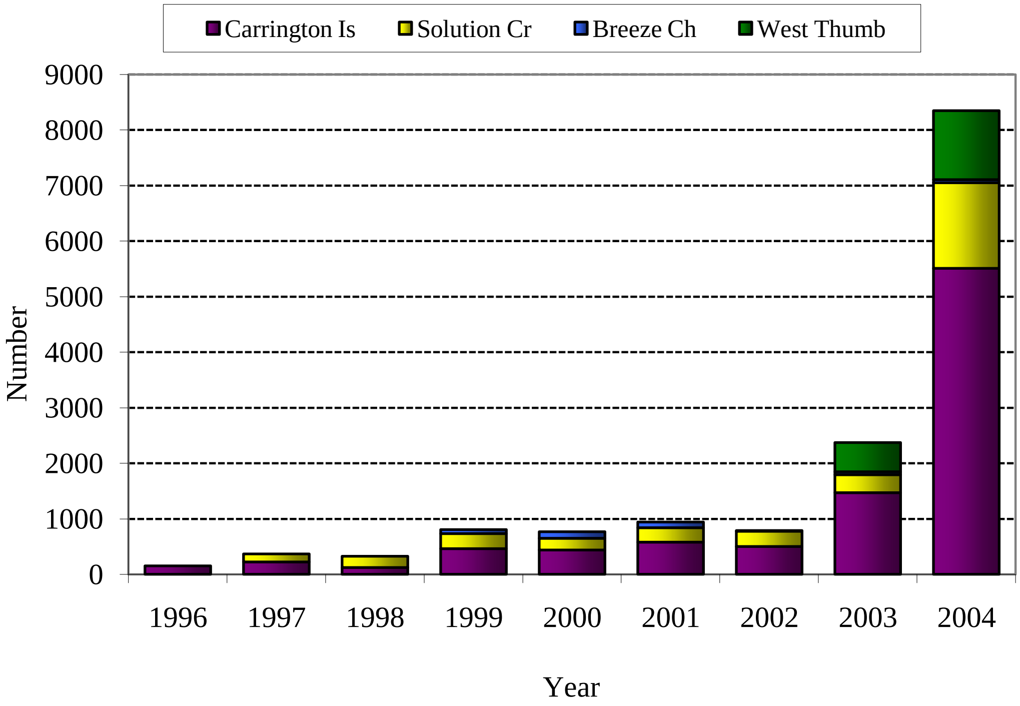

Figure 1-6. Number (bars) and mean total length (mm, line) of mature lake trout removed from Yellowstone Lake, Yellowstone National Park, Wyoming during spawning season, 1996-2004. Known spawning sites are located near Carrington Island, Solution Creek, and West Thumb Geyser Basin. Breeze Channel is thought to be a travel corridor for lake trout moving to spawning areas.

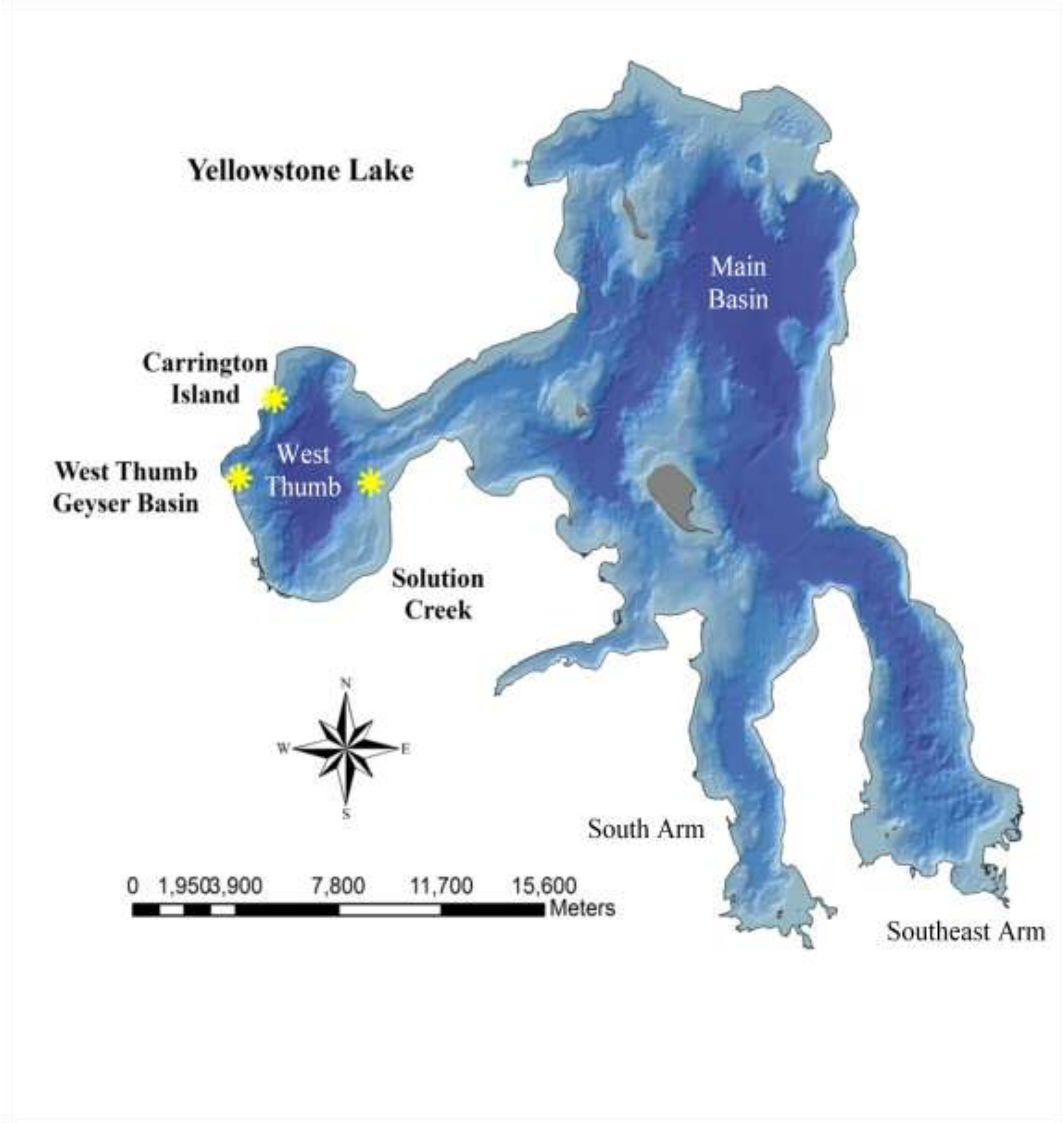

Figure 2-1. Three known spawning areas in Yellowstone Lake, all located in the West Thumb area of the Lake.

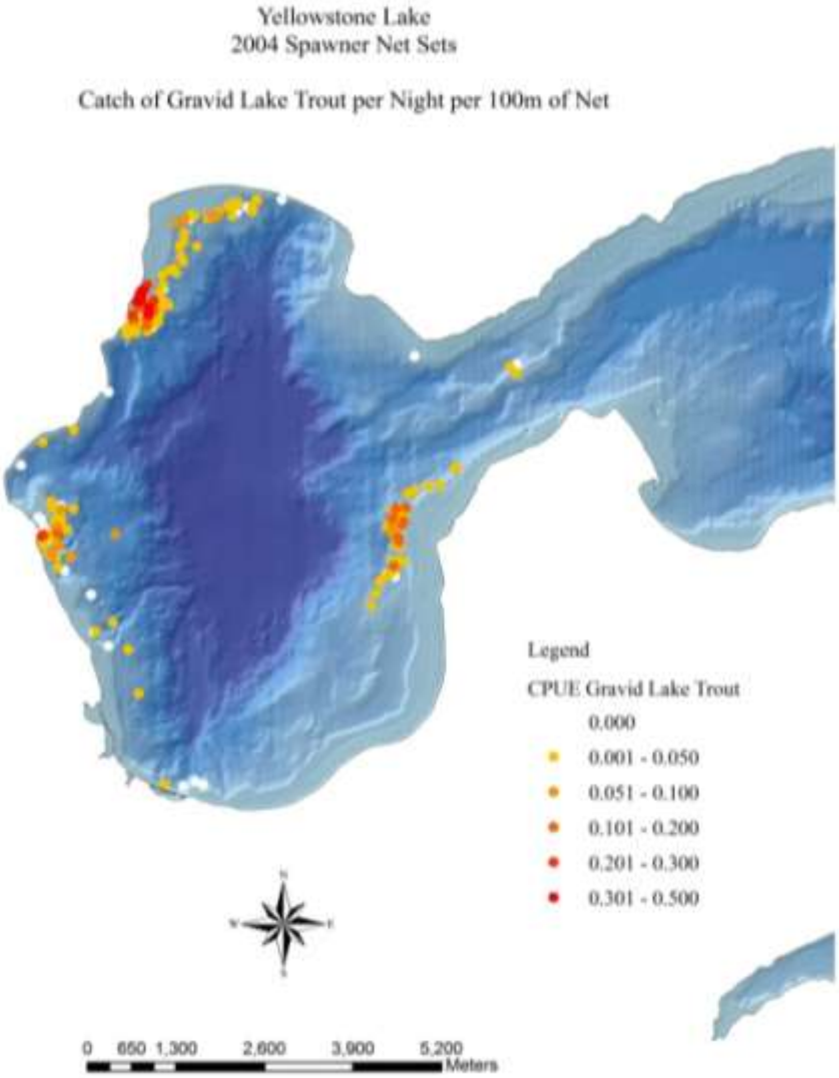

Figure 2-2. Catch per unit effort of gravid lake trout in Yellowstone Lake, Wyoming, 2004. All gillnet sets targeted at spawning lake trout are mapped; white dots represent areas where 0 gravid lake trout were captured, with progressively darker colors representing higher catch rates. Non-gravid lake trout catches are not represented. A unit of effort is equal to 100 m of net set overnight.

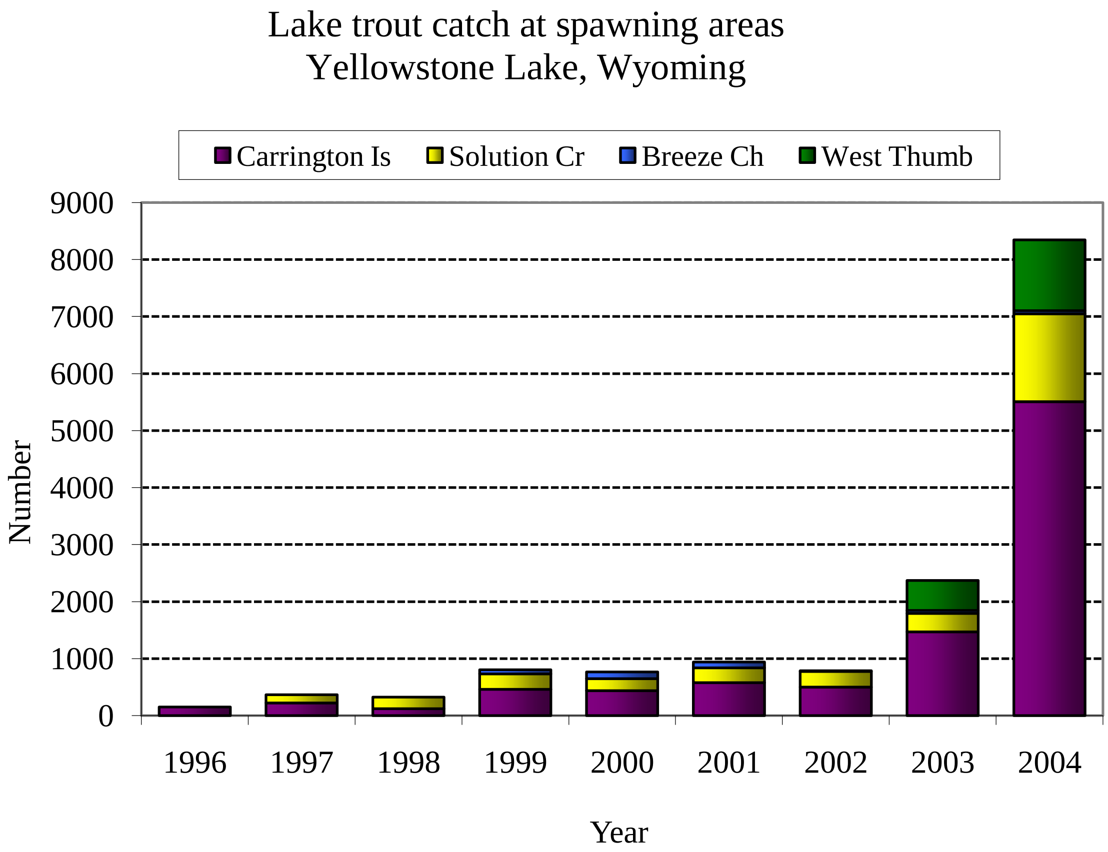

Figure 2-3. Catch of lake trout at known spawning areas, near Carrington Island, West Thumb geyser basin, and Solution Creek, by year, from 1996 through 2004, Yellowstone Lake, Wyoming.

Figure 2-4. Lake trout have been documented spawning in substrates found at either end of Carrington Island, located in the northeastern portion of the West Thumb of Yellowstone Lake, Wyoming.

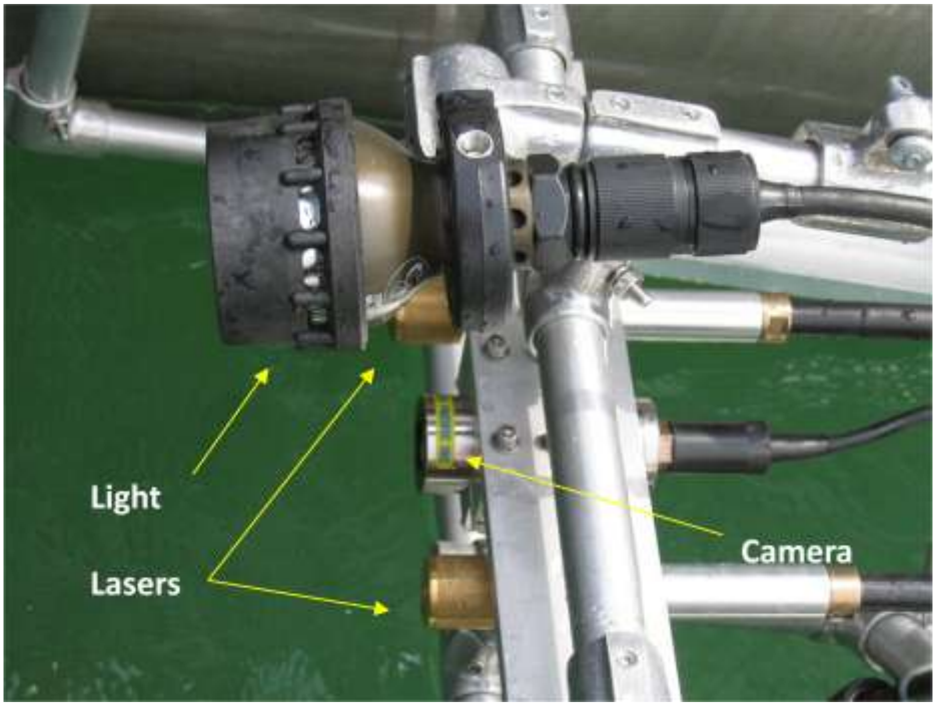

Figure 2-5. Underwater video camera with lasers and light. Lasers are set a known distance apart with the camera positioned in the center. This allows direct measurement of images in the view frame by calibrating the distance between the two images the lasers leave in the view. Lasers, light, and camera all are equipped with separate power switches to allow control of light in the view.

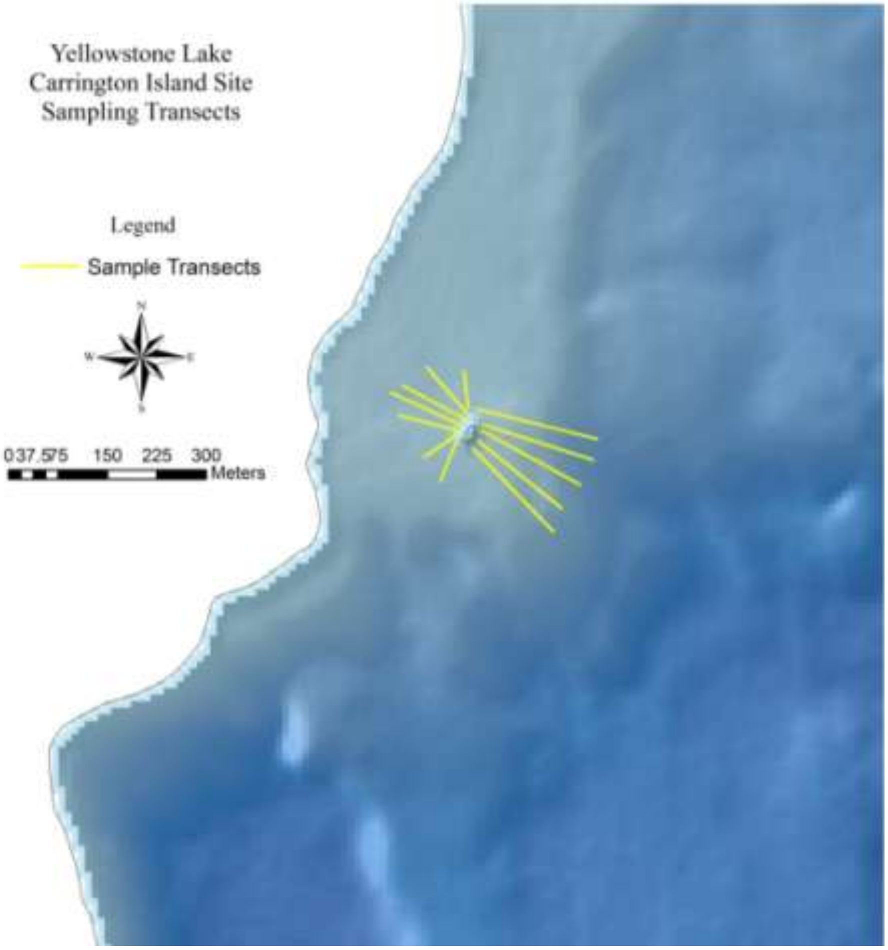

Figure 2-6. Sampling transects at the Carrington Island spawning area, Yellowstone Lake, Wyoming.

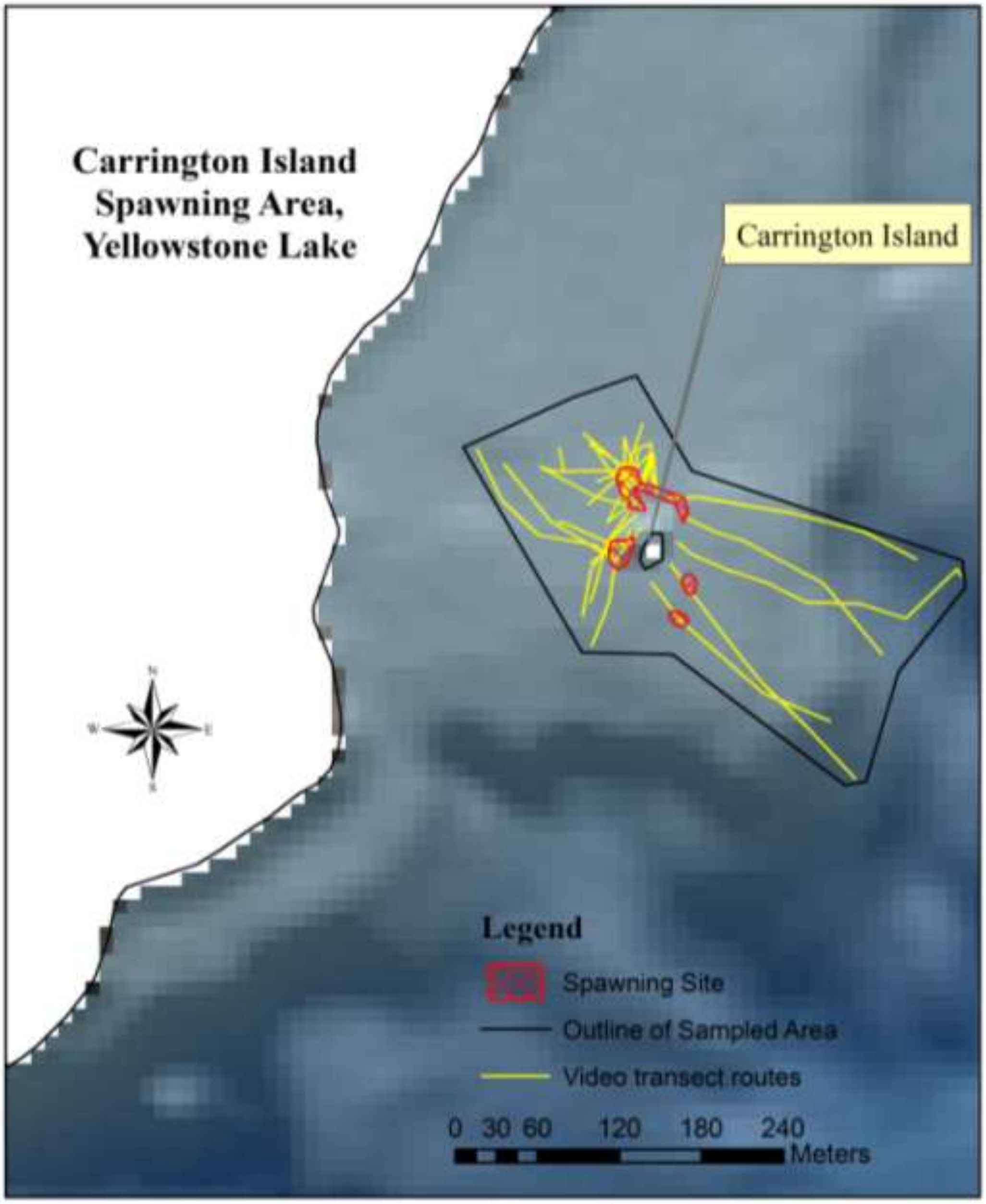

Figure 2-7. Actual boat path along designated and additional transects at Carrington Island spawning area, Yellowstone Lake, Wyoming.

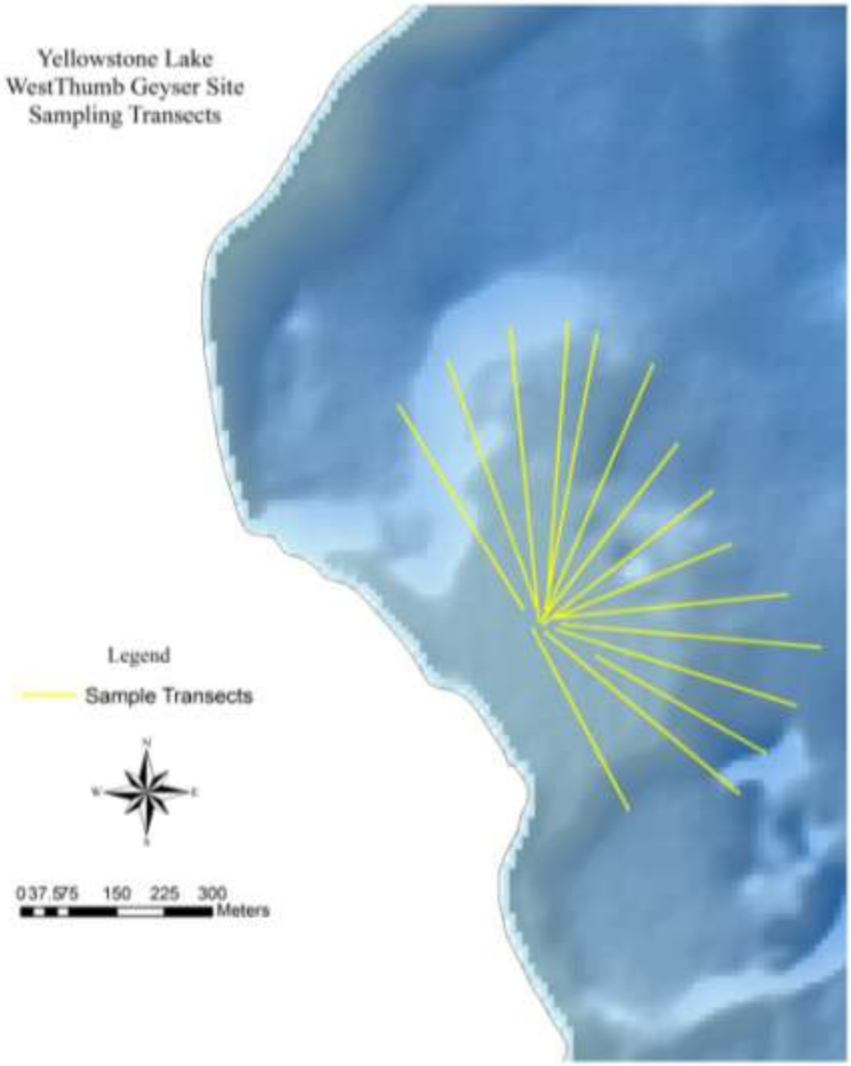

Figure 2-8. Sampling transects at the West Thumb geyser basin spawning area, Yellowstone Lake, Wyoming.

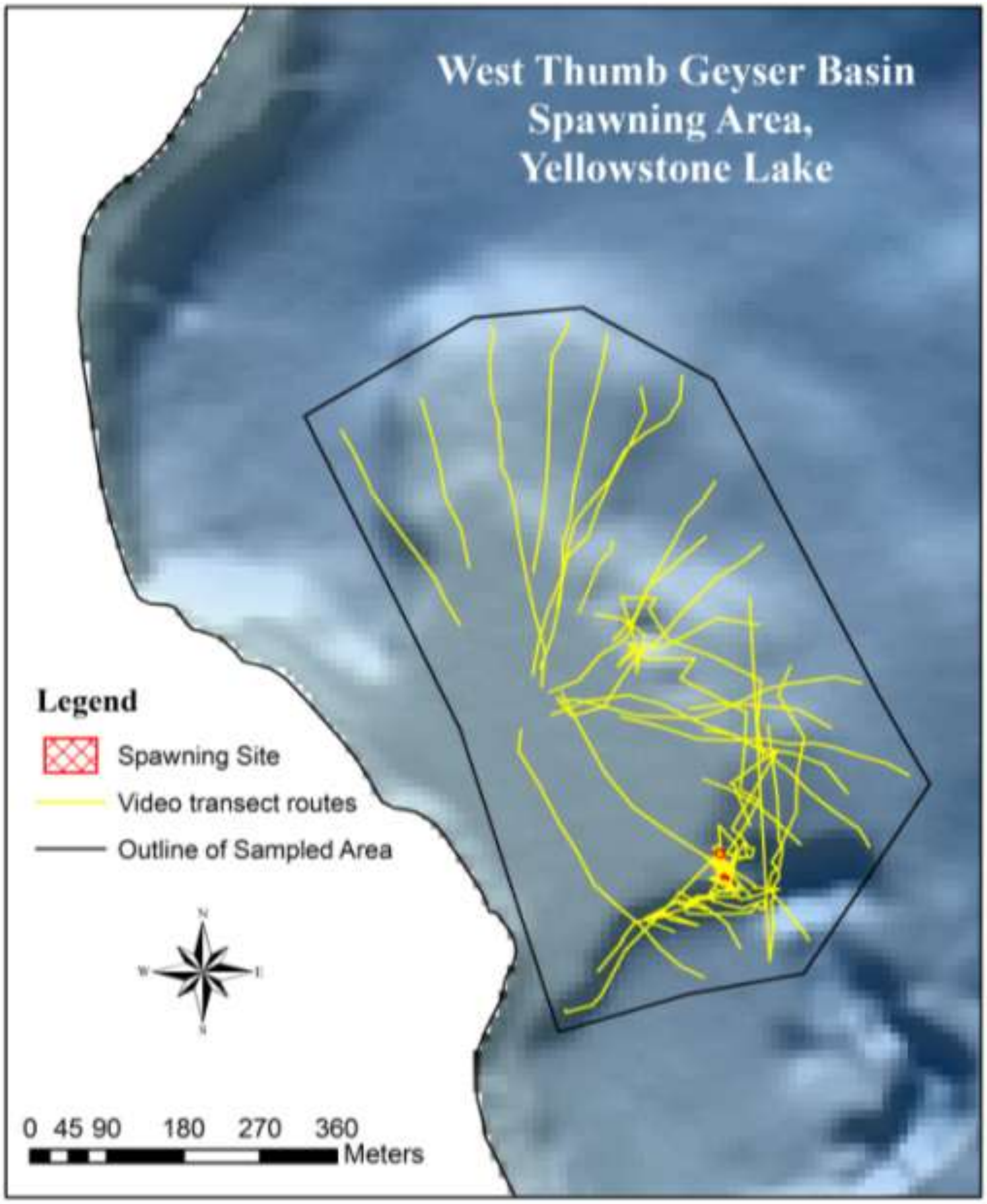

Figure 2-9. Actual boat path along designated and additional transects at spawning area near West Thumb geyser basin, Yellowstone Lake, Wyoming.

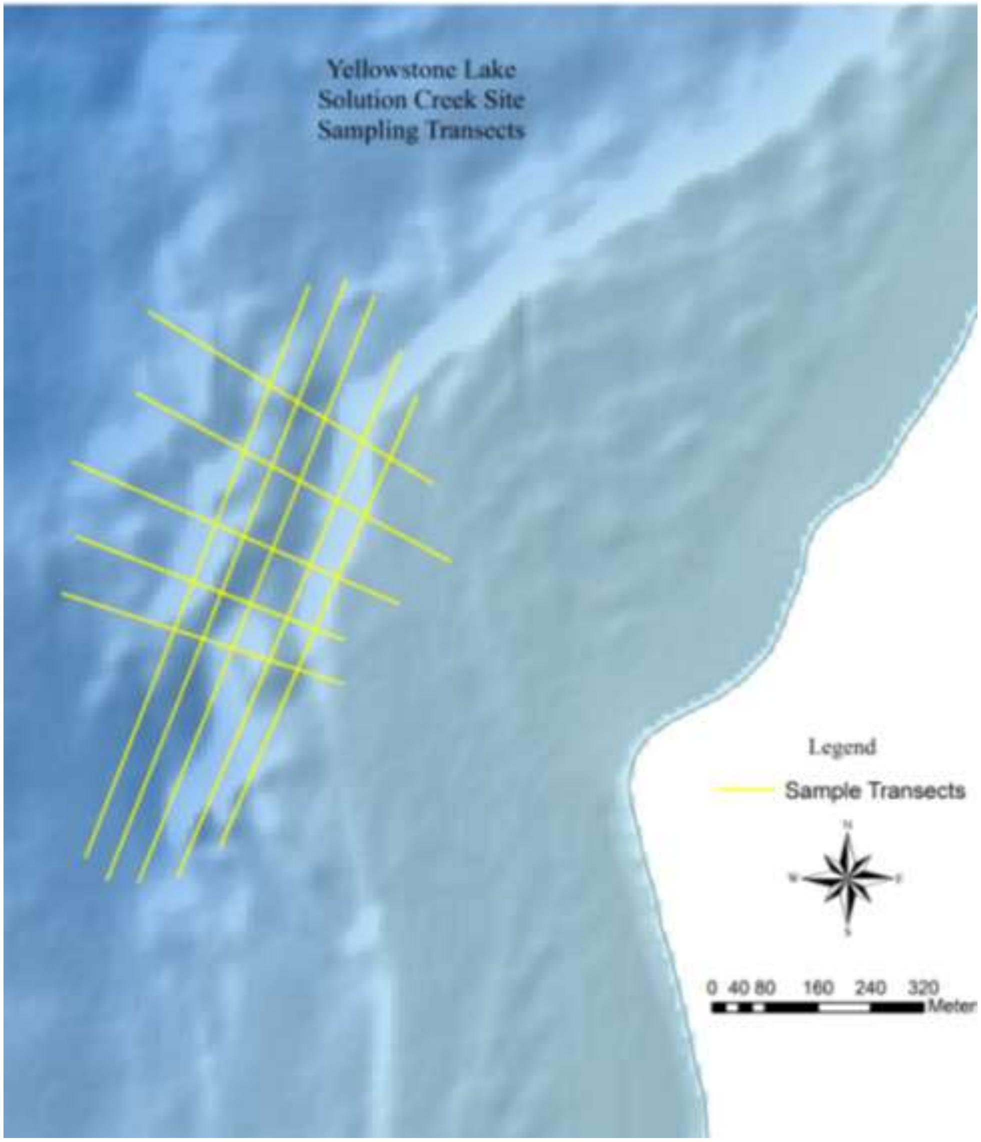

Figure 2-10. Sampling transects at the Solution Creek spawning area, Yellowstone Lake, Wyoming.

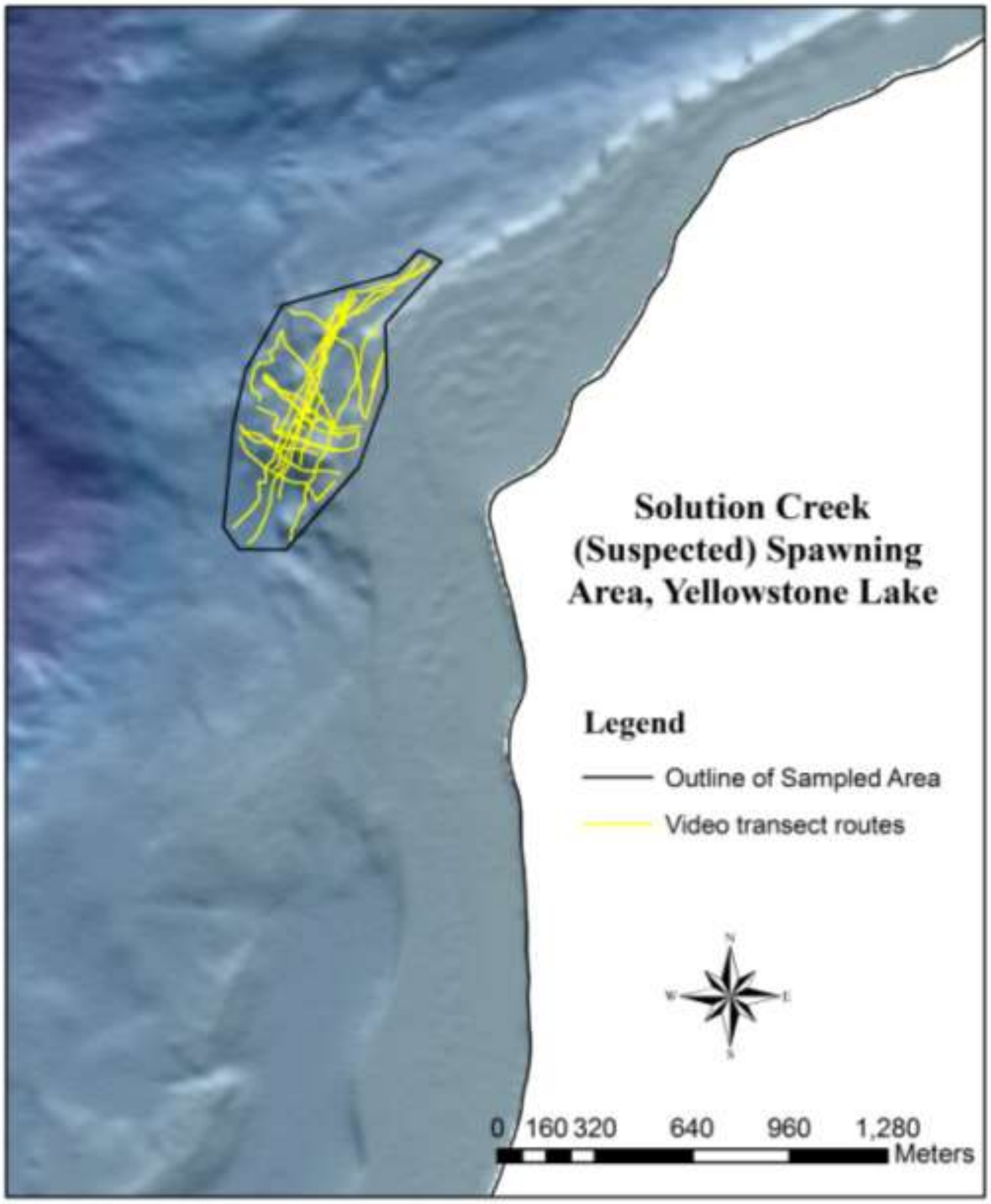

Figure 2-11. Actual boat path along designated and additional transects at the Solution Creek suspected spawning area, Yellowstone Lake, Wyoming.

Figure 2-12. Example of an anastomosing tubular structure from the floor of Yellowstone Lake, 2004. These features are found associated with active and inactive thermal vent fields throughout the lake.

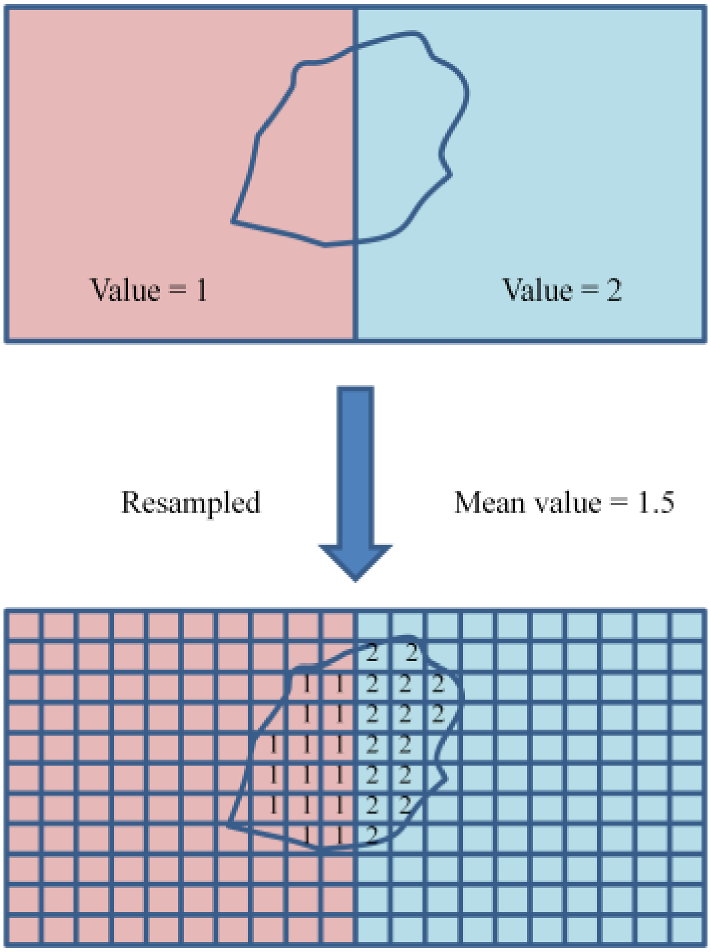

Figure 2-13. Prior to resampling, no value could be obtained for this polygon for this raster data set. After resampling a 10-m cell raster data set to 1-m cell size, mean value can be more accurately determined.

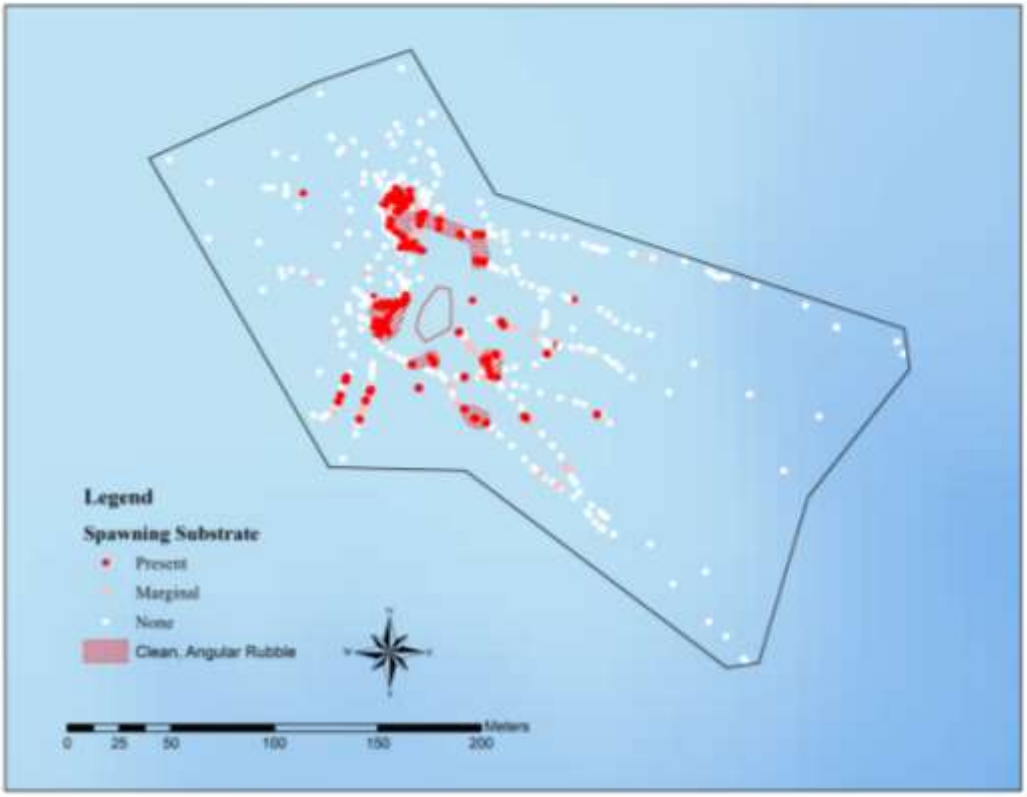

Figure 2-14. All snapshot locations taken along designated and additional transects with 5 areas of clean, angular rocky substrate suitable for lake trout spawning delineated, Carrington Island spawning area, Yellowstone Lake, Wyoming.

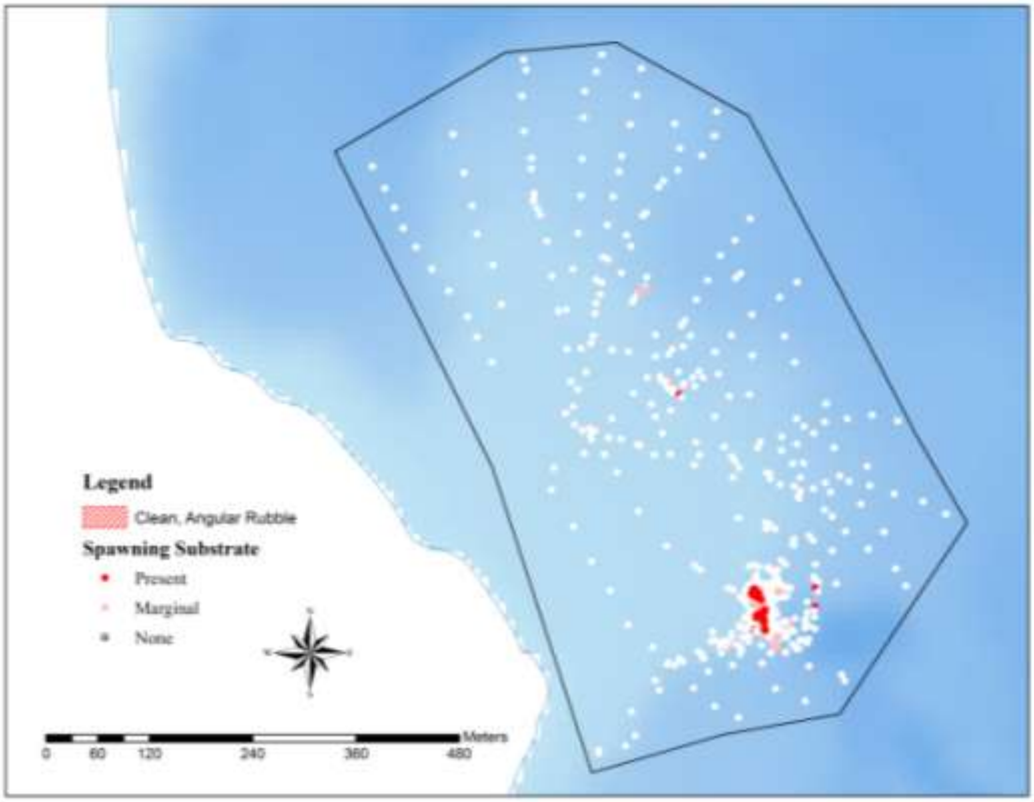

Figure 2-15. All snapshot locations taken along designated and additional transects with 2 small areas of clean, angular rocky substrate suitable for lake trout spawning delineated, West Thumb geyser basin spawning area, Yellowstone Lake, Wyoming.

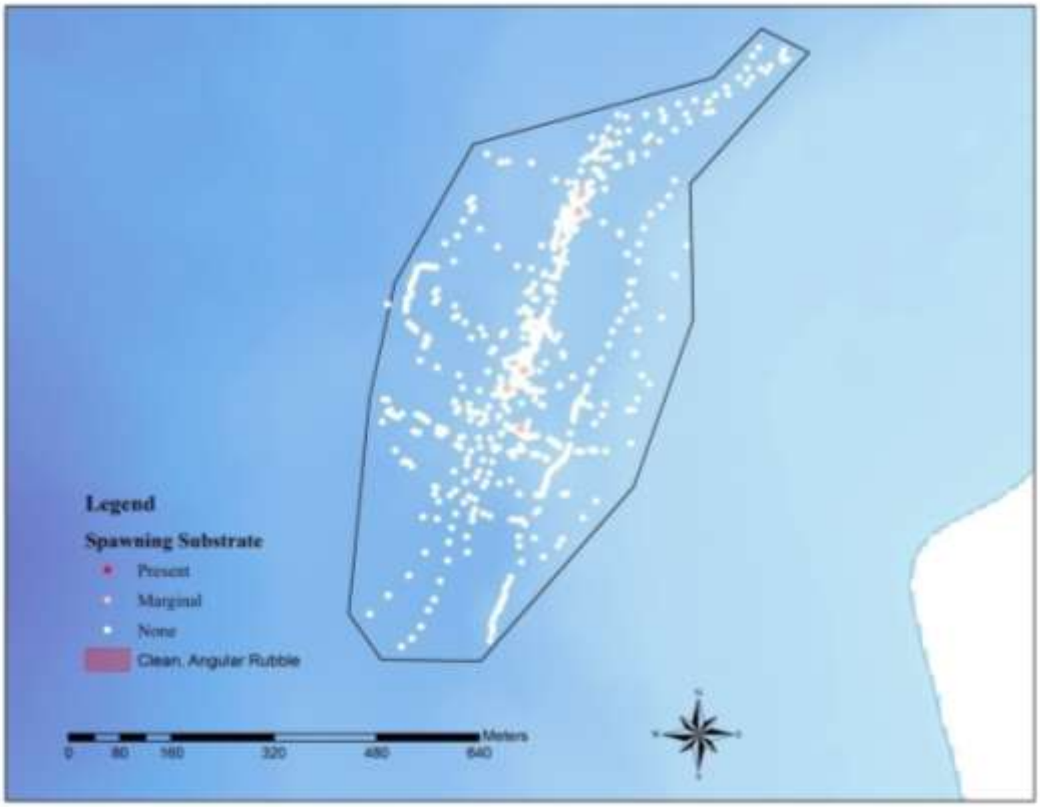

Figure 2-16. All snapshot locations taken along designated and additional transects, Solution Creek (suspected) spawning area, Yellowstone Lake, Wyoming. No areas with suitable spawning substrate were delineated.

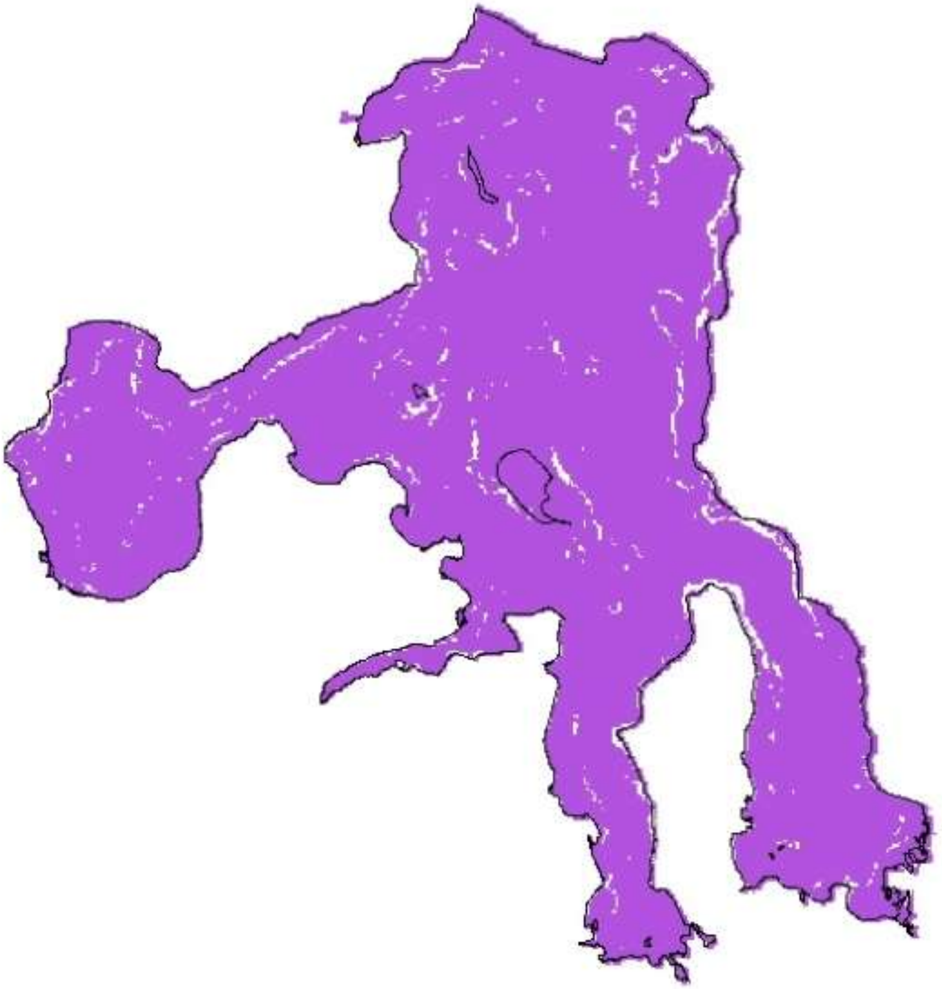

Figure 3-1. Slope of less than or equal to 45^o (purple) and greater than 45^o (white) for Yellowstone Lake, Wyoming.

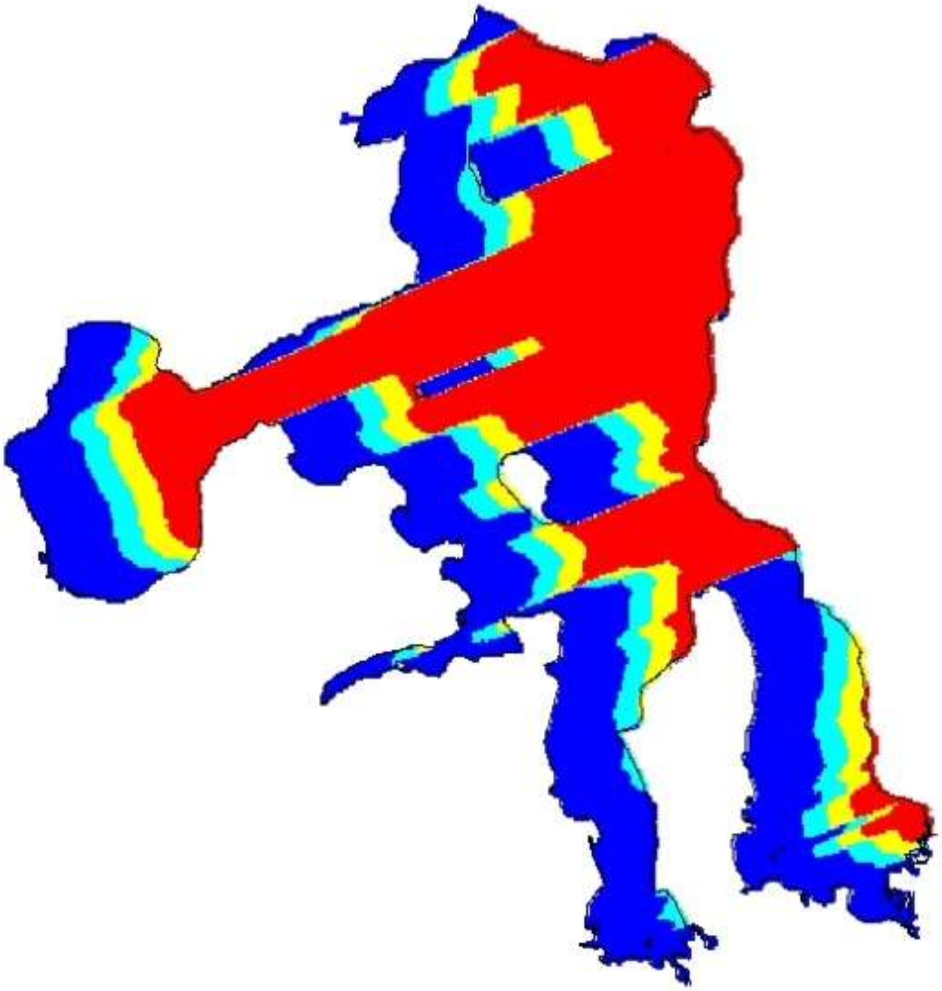

Figure 3-2. Resultant fuzzy fetch map of Yellowstone Lake, Wyoming. Fetch was calculated assuming wind direction of 247^{o} and fuzzy values were determined by equating values greater than 5 km as 0, less than or equal to 1.5 km as 1, and a straight-line equation for all values between. (Key: blue = 0.00 to 0.25, aqua = 0.26 to 0.50, yellow = 0.51 to 0.75, and red = 0.76 to 1.00)

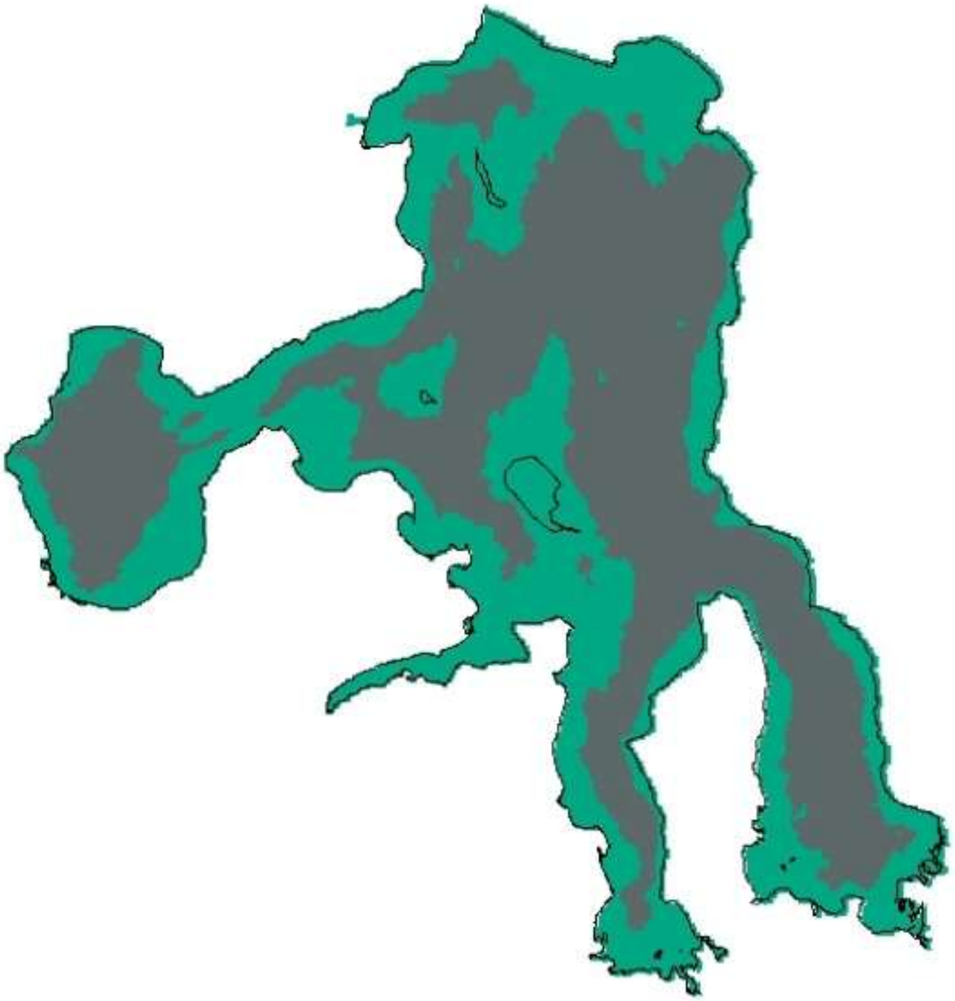

Figure 3-3. Depths less than or equal to 40 m (green) and those greater than 40 m (gray) for Yellowstone Lake, Wyoming.

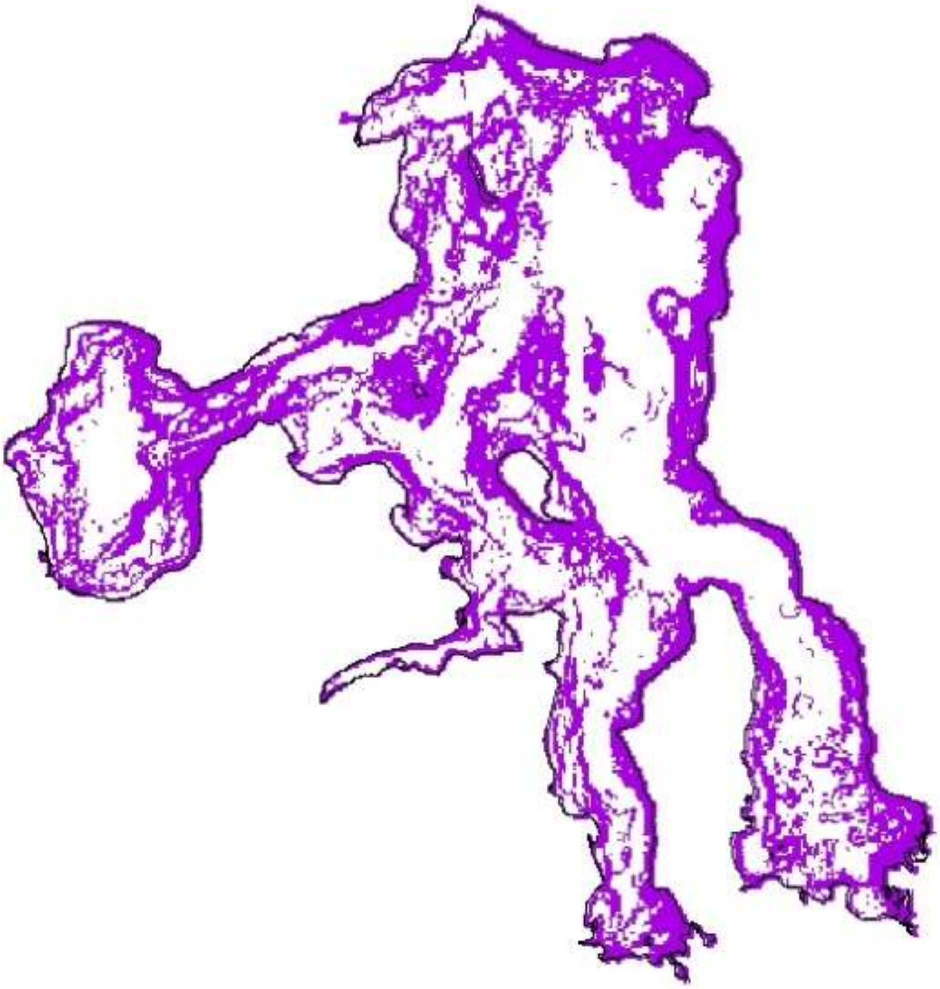

Figure 3-4. Erosive and transition zones (purple) of Yellowstone Lake, Wyoming, based on calculation of the deposition boundary (Rowan et al. 1992) and ± 1 m depth either side (Flavelle et al. 2002).

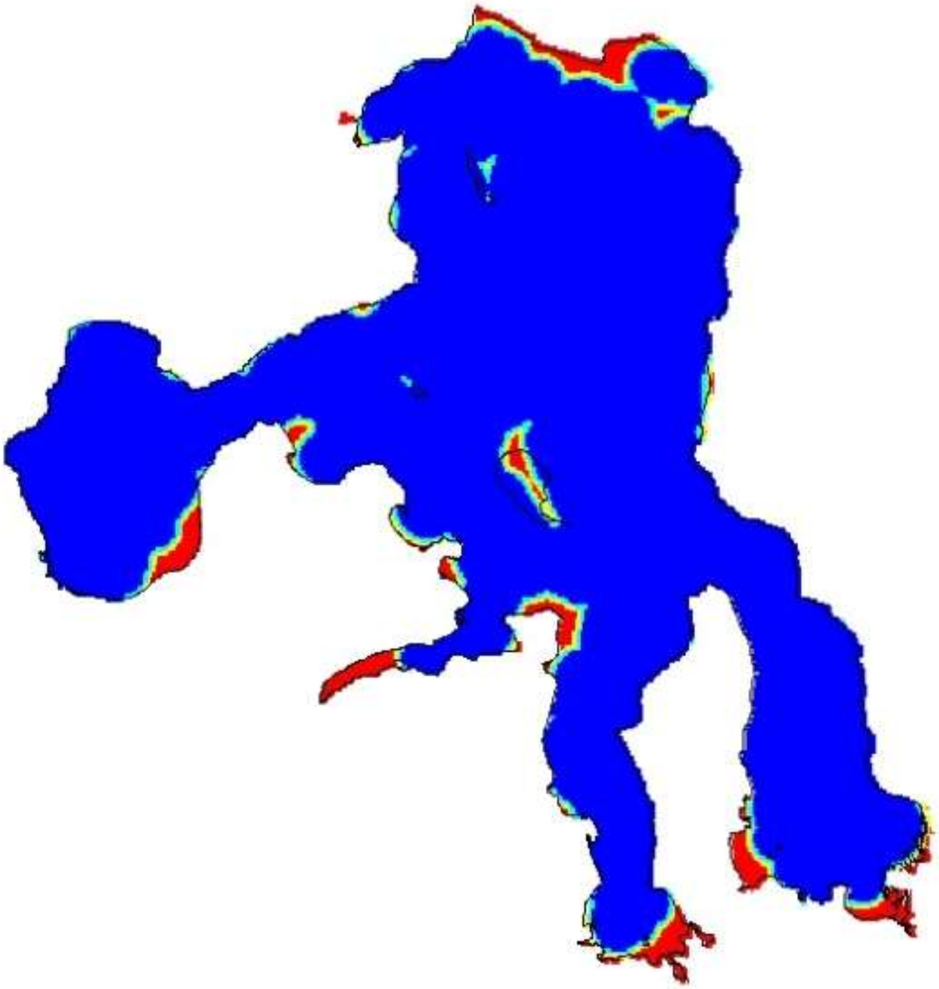

Figure 3-5. Distance to refuge of 30-m deep water in Yellowstone Lake as determined using Euclidean distances reclassified with fuzzy logic where blue represents full membership, decreasing downward to full exclusion represented by red.

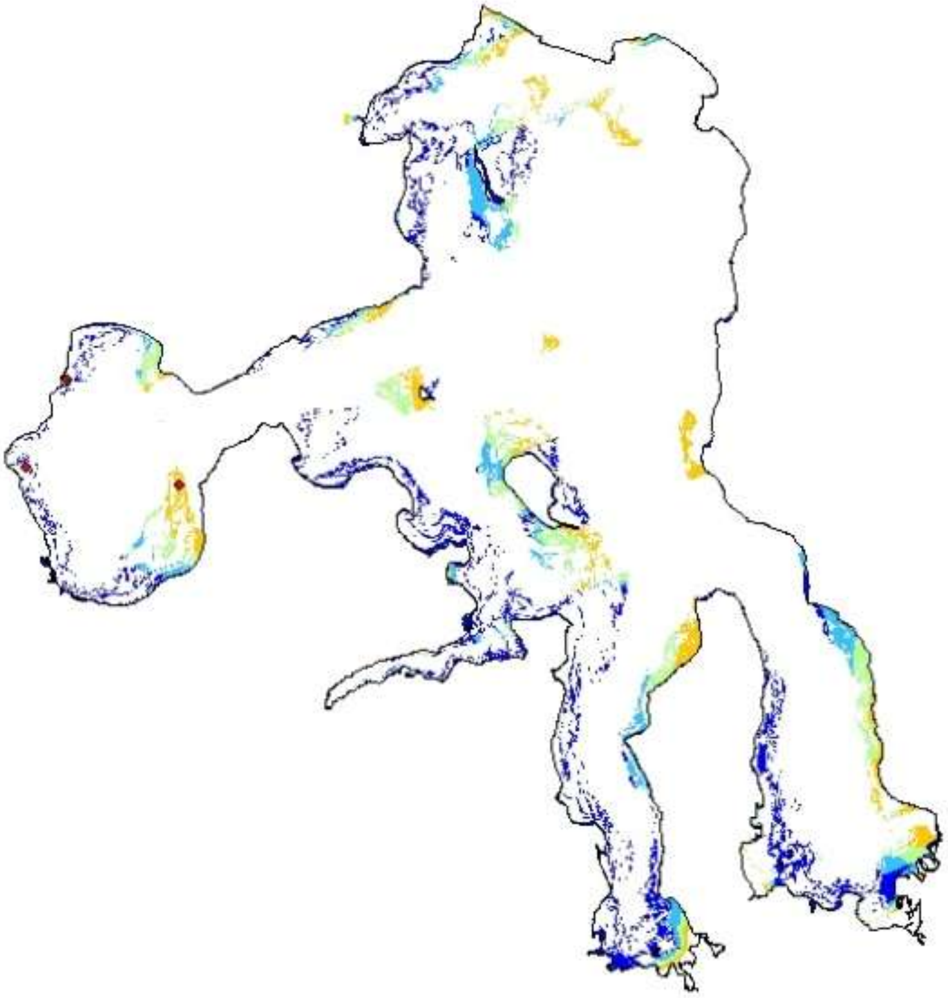

Figure 3-6. Initial habitat suitability index model with potentially excellent (dark blue), good (aqua), fair (light green), and poor (yellow) lake trout spawning habitat in Yellowstone Lake, Wyoming. Three suspected lake trout spawning areas in the western portion of the lake are marked with a red asterisk. Model parameters were based on values obtained from the literature and used with very simple combination techniques. Further refinement of the model will add greatly to its utility.

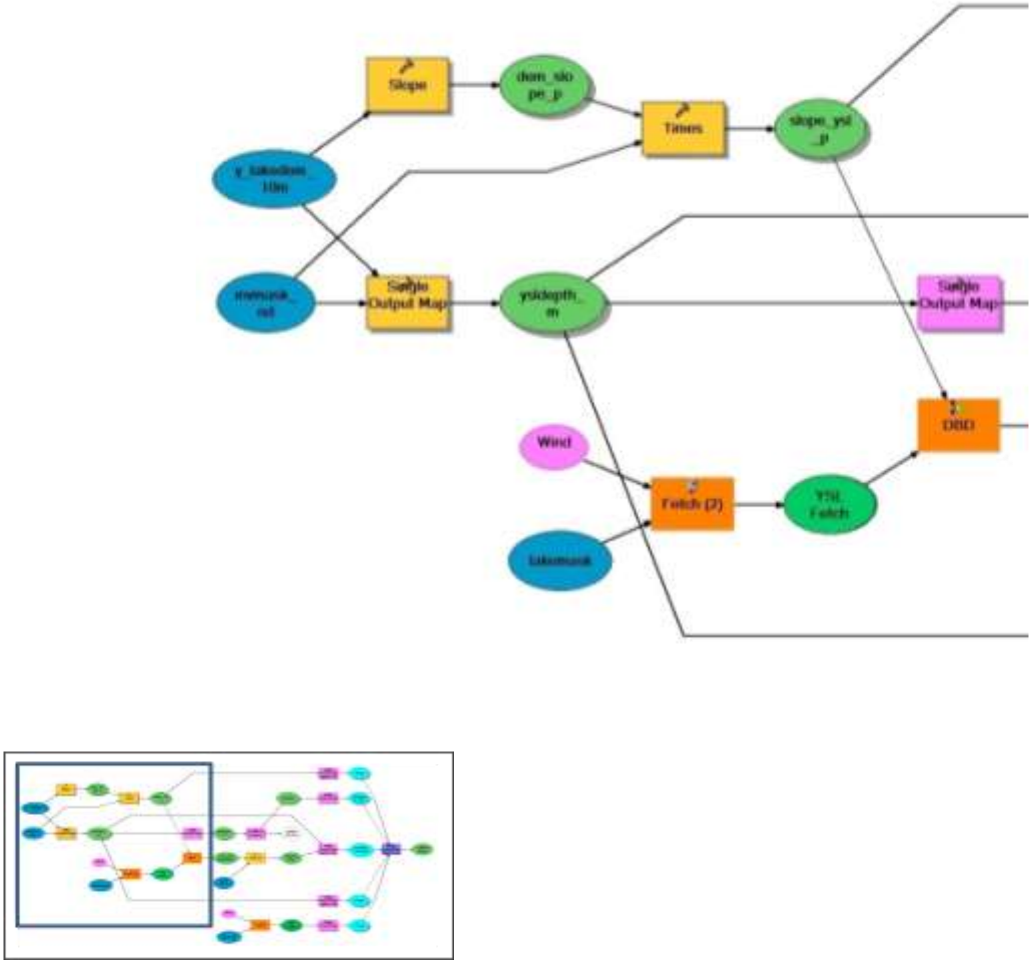

Figure 3-7 (continued on next page). Initial spawning habitat suitability index model for lake trout, Yellowstone Lake, Wyoming. Blue ovals represent data inputs, yellow boxes are data manipulation processes, green ovals are derived data, orange boxes are models within the model (for fetch and deposition boundary depth), and the violet box represents the last recombination and weighting process for the resultant model map. Pink ovals and boxes represent points where data can be manipulated through a range of values for sensitivity analysis and to affect the final map.

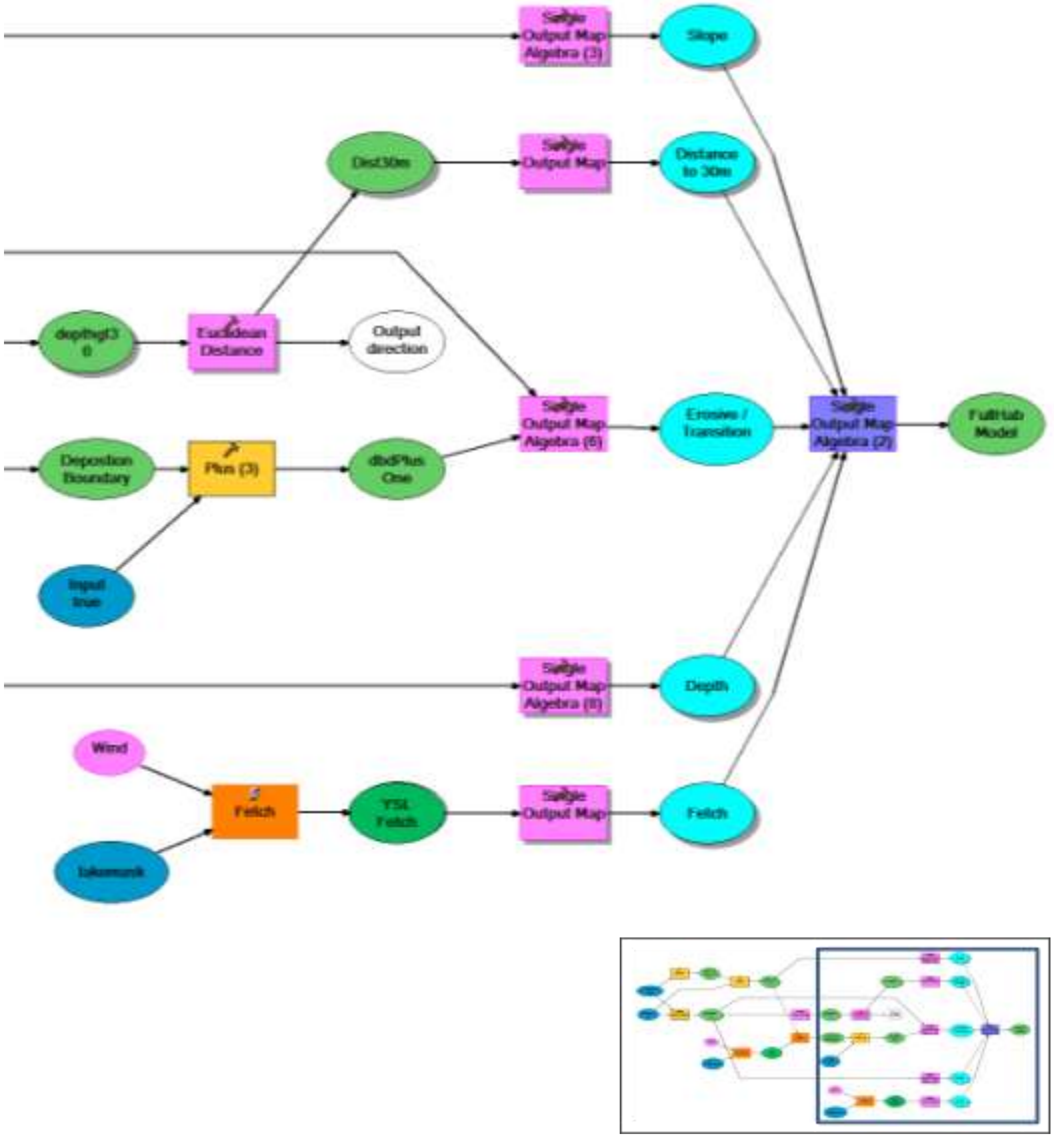

Figure 3-7 (continued). Initial spawning habitat suitability index model for lake trout, Yellowstone Lake, Wyoming. Blue ovals represent data inputs, yellow boxes are data manipulation processes, green ovals are derived data, orange boxes are models within the model (for fetch and deposition boundary depth), and the violet box represents the last recombination and weighting process for the resultant model map. Pink ovals and boxes represent points where data can be manipulated through a range of values for sensitivity analysis and to affect the final map.

Figure A-1. Towed vehicle with underwater video camera, underwater light, and two laser lights.

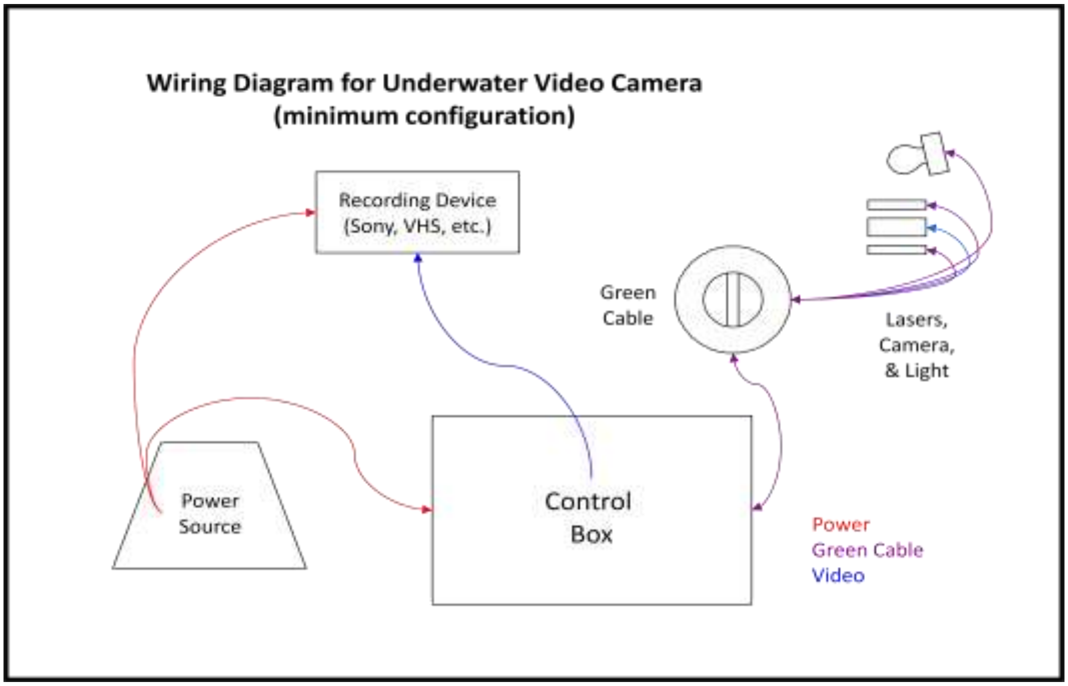

Figure A-1. Minimum configuration wiring diagram for underwater video camera, underwater light, and laser set-up.

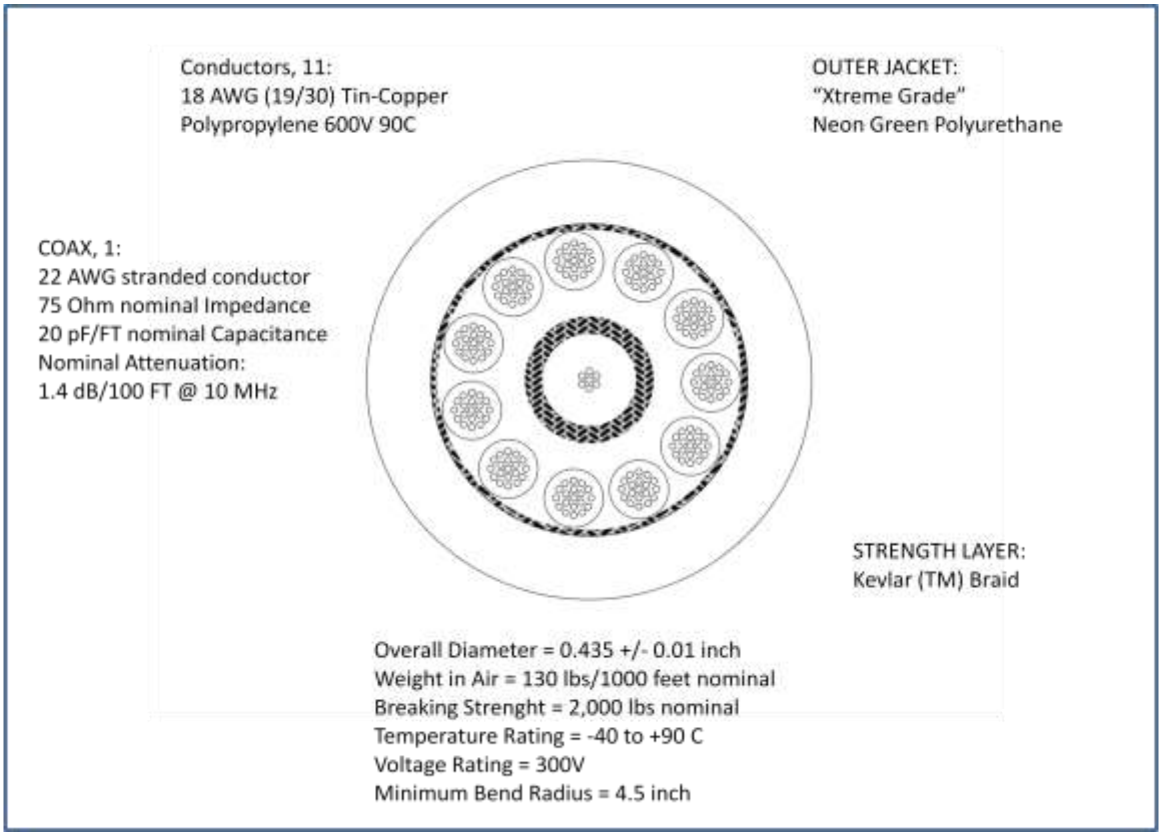

Figure A-2. Cable used to convey power to the lights, camera, and lasers, as well as to convey the video stream back to the surface.

Figure A-3. Deck-mounted winch used to raise and lower the camera/tow sled configuration.

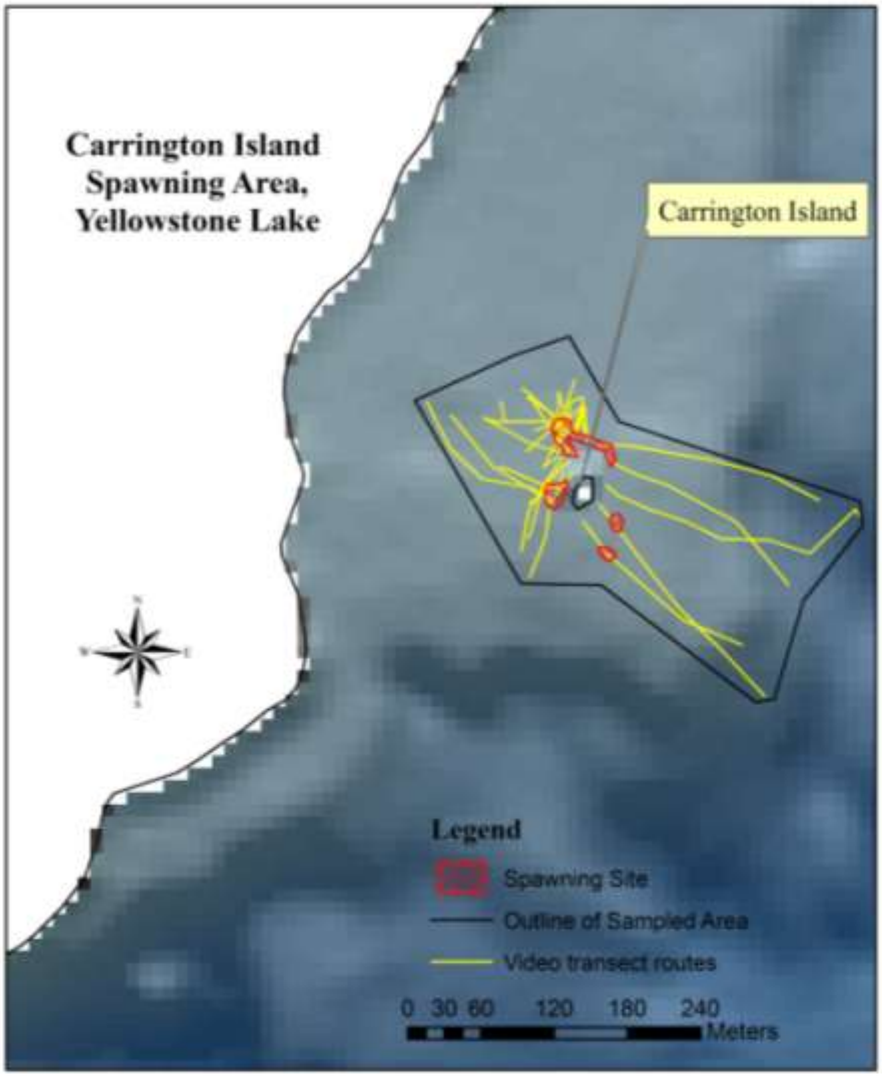

Figure A-4. Designation of spawning substrate (red) along transects (yellow) available to lake trout in near Carrington Island in Yellowstone Lake, Wyoming.

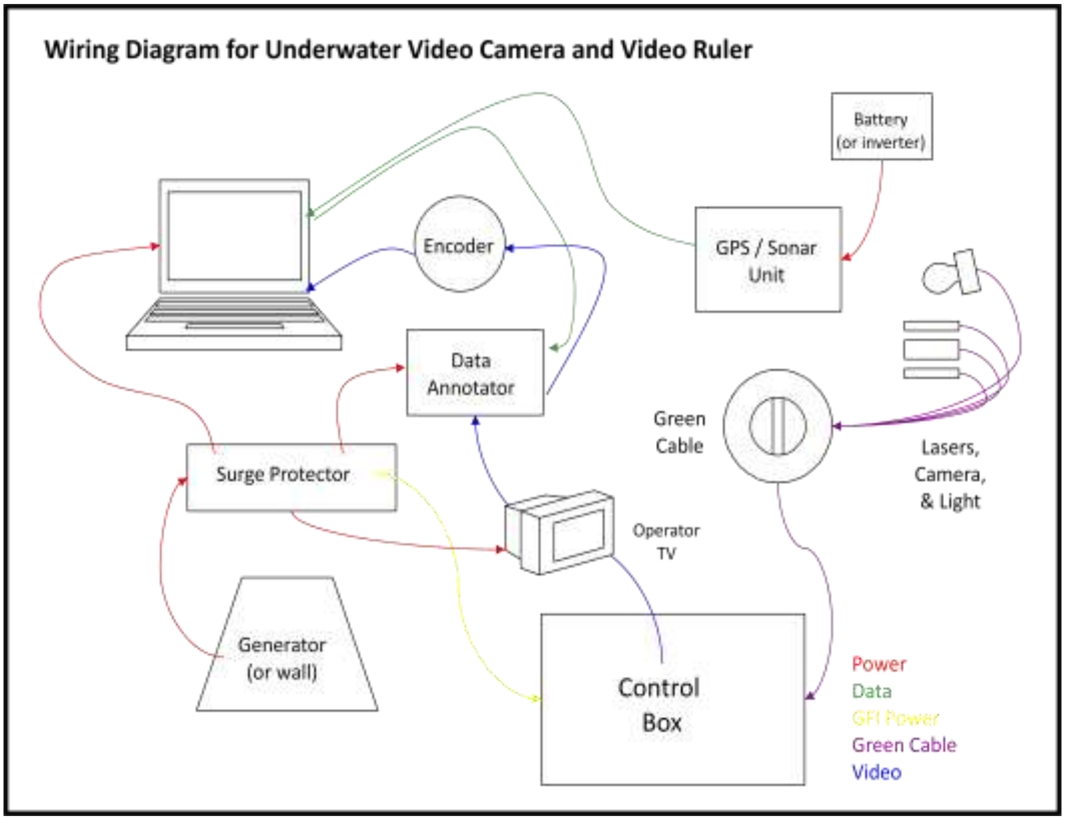

Figure A-5. Full wiring diagram for the underwater video camera, light, and lasers, including recording set-up for video and annotation of GPS location, water temperature and depth, and user text.