# Warm-Water Non-Native Fishes in Lake Tahoe

**Prepared for**

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## Introduction

Prior to large changes in community structure and nutrient concentrations, Lake Tahoe's community assemblage was relatively simple with 12 orders of zoobenthic taxa, 6 zooplankton species, and 8 fish taxa (Miller 1951, Frantz and Cordone 1970, and Vander Zanden et al. 2003b). The pre-invasion fishery (1872) was dominated by a single predator, Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). This trout grew to a large size (14 kg), utilizing primarily pelagic chubs (*Siphatales bicolor pectinifer*) and native zooplankton as their food source (Vander Zanden et al 2003b, Chandra et al 2005).

During the last 130 years numerous non-native species have been introduced intentionally and unintentionally to the Tahoe Basin, altering its biological assemblage. The first series of introductions occurred at the end of the 19$^{th}$ century. They included nine species of salmonids, thought to be suited to Tahoe's environment. Only rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and brook trout (*S. fontinalis*) survived and persist in the basin today. Predatory impacts from lake trout combined with over fishing, hybridization, and siltation of spawning streams contributed to the extirpation of Lahontan cutthroat trout from Lake Tahoe by 1939 (Cordone and Frantz 1968, Moyle 2002). Crayfish (*Pacifastacus leniusculus*) were introduced multiple times to Lake Tahoe and established by 1936. By the late 1960's numbers of crayfish were estimated up to 55 million. Studies suggest that under low densities (0.16 adult per m$^2$), crayfish stimulate periphyton productivity by removing old senescent cells (Abrahamsson and Goldman 1970, Flint 1975). Higher densities (1.07 adults per m$^2$) however result in decreased periphyton production (Abrahamsson and Goldman 1970). At either density, crayfish have been found to excrete nitrogen and phosphorus which are important stimulators of primary production. Today crayfish no longer contribute as a food source to the energetics of non-native lake trout except for the largest size classes (>50 cm). They are thought however to support the lake's newest fish invaders, largemouth bass.

The establishment of non-native kokanee salmon (*O. nerka*) occurred in 1945 and has since been supported through stocking for recreational opportunities. In the 1960's, state fish and game agencies introduced another invertebrate, *Mysis relicta*. The establishment of Mysid shrimp corresponded with shifts in the trophic niches of native tui chubs (*Gila bicolour obesa* and *Gila bicolour pectinifer*), kokanee, and the top predator lake trout. Both chub species decreased in trophic position as a result of feeding shifts to *Mysis,* which was further supported by their increased utilization of pelagic energy (Vander Zanden et al. 2003b). As a result of the strong restructuring of the zooplankton community due to Mysid predation on native cladocerans (Richards et al. 1975, Goldman et al. 1979, Threlkeld et al. 1980, Morgan et al. 1981) the energetics for kokanee salmon shifted resulting in a decrease in annual length and weight of returning spawners, probably due to exploitative competition with *Mysis* for cladocerans (Morgan et al. 1978). *Mysis* introduction also corresponded with a feeding shift of Lake Tahoe's dominant predator, lake trout, to pelagic energy sources. Large lake trout did not reduce their trophic position after *Mysis* invasion but shifted to more pelagic resources, which indicated a mix of *Mysis* and pelagic forage fish in their diet. Smaller lake trout size classes (13 cm and smaller) shifted to *Mysis* (Thiede 1997). After *Mysis* introduction, a 10-fold decrease in the abundance of forage fishes was documented (Thiede 1997) which indicated a potentially strong role of this non-native invertebrate in restructuring food web interactions and lake energetics. Growth rates of lake trout before and after Mysid introduction do not appear to have changed except for smaller size classes of fish.

In addition to non-native stocking and illegal introductions by humans, one of the leading drivers of biological invasions is climate change (Shuter and Post 1990; King et al. 1999; Lockwood et al. 2007). Introduced warm-water species cannot naturalize unless conditions support survival and reproduction. Warming can shift habitat suitability outside of a native species optimal range (Fausch et al. 2001), and ultimately relax abiotic and biotic conditions that normally inhibit non-native species (Dukes and Mooney 1999). Aquatic ecosystems are particularly at risk of climate-mediated biological invasions. Many aquatic organisms are ectotherms, thus their physiology, bioenergetics, and distribution are explicitly linked to temperature. Shuter and Post (1990) found climate delineated northern boundaries of the ubiquitous smallmouth bass, indicating that climate can regulate warm-water species distribution. Warm-water fishes positively respond to warming with increased spawning, growth, and reduced mortality (Coutant 1977; Shuter and Post 1990; King et al. 1999). For example, a 5 year-old largemouth bass can increase its weight by ~16 % with a 2 °C rise in annual air temperature (McCauley and Kilgour 1990). In addition, consumption rates and predation pressure can increase with temperature, as was the case for non-native piscivores predating native salmonids in the Columbia River (Petersen and Kitchell 2001).

Temperature increases in aquatic habitats are projected to occur over the long term (Solomon et al. 2007), which will relax climatic constraints for warm-water fishes increasing establishment success, and elevating concern for native species and food-webs in northern water bodies (Winder and Schindler 2004; Rahel and Olden 2008; Rahel et al. 2002) such as Lake Tahoe.

***Recent Invasive Species***

*Invasive plants*

Until 1994, no comprehensive surveys for rooted aquatic plants had been conducted in the lake. Early reports (1975) of water milfoil (*Myriophyllum* spp.) near

Taylor Creek did not identify whether it was a native or non-native species. Large densities of the plant are thought to pump generally unavailable nutrients such as phosphorus from the sediments into the water column, thereby increasing algae production, and decreasing clarity. Furthermore, plants can create habitat for non-native fishes and clog boat propellers. Severe impacts from aquatic plants were observed in Tahoe Keys by the end of the 1970's and early 1980's, during which time mechanical harvesting was begun.

With the potential invasive threats in mind, the US Department of Agriculture/ Agricultural Research Service conducted surveys periodically from 1995 to 2006 (Anderson and Spencer 1996). The most recent USDA-ARS survey of the entire 114 km lake shoreline was completed in the fall, 2006. The ten year trend is clear: populations of invasive Eurasian water milfoil (*M. spicatum*), coupled with the more recent (2004 - 2008) spread of invasive curly leaf pondweed (*Potamogeton crispus*) are expanding. Invasive milfoil is now present in abundance in most of Tahoe Keys and in over 30 locations outside the Keys, including new infestations (compared to 2003) along the western shore, south of the Lower Truckee River outlet, at the mouth of the Lower Truckee River, and in the Truckee River. Pondweed is prevalent and spreading along the southern shoreline from the western Keys channel east to Lakeside Marina. It is exhibiting typical range-expansion into areas without vegetation as well as those with invasive milfoil and native pondweed species. The expansion appears to be following an eastward flow of both water currents and wind. Pondweed has not currently spread further west and north on the California side, or much further north than Lakeside Marina. The largest populations are at Ski Run and the channels at Tahoe Keys. However, based on the fall, 2006 survey, it appears that new colonies are rapidly becoming established. It's likely that densities along the entire south shore will increase with each growing season unless management actions are taken.

*Invasive fishes*

In the mid to late 1970's and again in the late 1980's, a variety of non-native fish species were found in the nearshore environment (Reuter and Miller 2000). The warm-water fish introductions were illegal and thought to be the result of anglers eager to catch these fish. At this point warm-water fish species were rarely found around the lake while native minnows remained abundant. By the end of the decade, non-native largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) were common while native Lahontan redside (*Richardsonius egregius*) and speckled dace (*Rhinichthys osculus*) populations declined or were virtually eliminated from Tahoe Keys, an important rearing ground for native fishes (DFG, unpublished data). The change in fish structure was confirmed by fishing guides operating out of Tahoe Keys. Within a decade they could no longer collect minnows commonly used as bait during fishing charters from certain marinas. The quick reduction in native fish abundance has raised alarm especially as suitable habitat for non-native fishes is expanding.

The lack of mixing between marinas and the main part of the lake facilitates the invasion of non-native plants and crayfish which provide habitat and food for non-native warm-water fishes. Marinas and embayments experience elevated water temperatures throughout summer months conducive to survival and establishment of warm-water species. This, combined with Lake Tahoe's warming trend (Coats et al. 2006) will expand thermally suitable habitat and increase growth periods for these recent invasive fishes. Recently, small satellite populations of largemouth bass have appeared around Lake Tahoe and are likely sourced from the marina population (Kamerath et al. 2008).

Bass populations in Lake Tahoe are currently supported by elevated temperatures in marinas and bays, and patches of non-native aquatic vegetation (Reuter and Miller 2000; Ngai 2008). Although colonization can take several years, recent studies suggest that Lake Tahoe is warming, which may promote bass expansion by increasing thermal suitability of habitats and opening migration corridors between them. Coats et al. (2006) found deep pelagic waters have warmed in the last 30 years, and surface water temperatures are expected to increase ~3 ˚C by 2099 (Ngai 2008). Previous research indicates that bass persistence in Lake Tahoe will threaten native littoral fishes and food-web function (Kamerath et al. 2008). Thus, as climate warming escalates warm-water species' expansion throughout Lake Tahoe it is important to identify where establishment is highly likely, to minimize management costs and protect Lake Tahoe's remaining native fishes.

In other ecosystems, warm-water non-native fish species threaten to further reduce food web efficiency and decrease native biodiversity of fish assemblages (MacRae and Jackson 2001). Forage fish communities have shifted, declined in abundance, and decreased in biodiversity in lakes after large and smallmouth bass introductions (Betolli et al. 1992, MacRae and Jackson 2001, Vander Zanden et al. 2003a). Previous studies show introduction of top predators such as largemouth bass have threatened the persistence of cyprinids, and other piscivores such as lake trout (Whittier et al. 1997; Jackson 2002). Species richness of littoral fishes in Adirondack lakes with introduced largemouth bass compared to lakes without was significantly lower (Findlay et al. 2000). Moyle and Nickols (1973) found that bluegill presence in Sierra Nevada foothill streams were negatively correlated with percent of native fish present. Fish introductions are not without economic cost either. It is estimated that non-native fish introductions in the U.S. have caused an annual loss of 1 billion dollars (Pimentel et al. 2000).

In an effort to prevent and control proliferation of warm-water invaders in Lake Tahoe, our objectives were to: a) determine current distribution and relative abundance of warm-water non-native species within Lake Tahoe, b) collect basic ecological information from 2 established populations in Tahoe Keys and Taylor creek, c) develop empirical predictive models that reconstruct historical and predict future surface water temperatures of Lake Tahoe under climate change scenarios (increase in atmospheric $CO_2$ : 635-686 ppm), d) identify where in Lake Tahoe's nearshore largemouth bass are likely to establish given current conditions of temperature and habitat (vegetation), e) estimate how predation pressure on native fishes will vary among those locations, and f) determine the movement of warm-water non-native species in Tahoe Keys to determine if this location may be the source populations to other locations in the lake.

## Methods

### *Study Site*

Lake Tahoe (39° N 120° W) is a sub-alpine oligotrophic lake in the Sierra-Nevada mountain range bridging California and Nevada, USA. Our study was conducted from 2006 to 2008 at several locations on the Lake Tahoe shoreline (Table 1, Figure 1). In 2006, 20 sites were surveyed around the lake. New sites were added in 2007 and 2008 with the omission of some previously sampled sites (Table 1 and Figure 1). We performed bi-weekly snorkeling surveys at all our sites between May and Nov with some exception. In 2006, Cave Rock, Sand Point and Sand Harbor were only snorkeled irregularly due to access issues. In 2008, low lake water level

Table 1. Sites monitored during bi-weekly snorkel survey in 2006, 2007, and 2008 with GPS coordinate. Sites are classified as enclosed (E) or Open (O). See text for further definition.

| Site | Enclosed (E) or Open (O) site | GPS Coordinate |
|---|---|---|
| Tahoe Keys Marina (East) | E | N38 56.069; W120 00.137 |
| Tahoe Keys Home (West) | E | N38 55.744; W120 00.898 |
| Taylor Creek | E | N38 56.413; W120 03.409 |
| Emerald Bay | O | N38 57.1117; W120 06.225 |
| Meeks Bay[a] | E | N39 02.212; W120 07.379 |
| Obexer | E | N39 04.923; W120 09.446 |
| Sunnyside | E | N39 08.340; W120 09.183 |
| Tahoe City Marina | E | N39 10.310; W120 08.209 |
| Tahoe City Non-Marina[b] | O | N39 10.1759; W120 08.1630 |
| Lake Forest[b] | O | N39 10.5012; W120 07.1214 |
| Star Harbor[c] | E | N39 10.956; W 120 07.135 |
| Carnelian Bay | E | N39 13.595; W 120 04.888 |
| Crystal Bay | O | N39 14.900; W119 59.075 |
| Sand Harbor | O | N39 12.393; W119 55.837 |
| Sand Point | O | N39 10.573; W119 55.690 |
| Cave Rock | O | N39 00.2682; W119 57.0053 |
| Zephyr Cove | O | N39 00.426; W 119 56.998 |
| Elk Point[c] | E | N38 59.01; W119, 57.13 |
| Round Hill Pines | E | N38 59.2379; W119 57.1445 |
| Lakeside | E | N38 57.3247; W119 57.0662 |
| Ski Run | E | N38 57.023; W119 57.565 |
| Timbercove | O | N38 56.871; W119 58.007 |

[a] Not sampled in 2008

[b] Not sampled in 2007 and 2008

[c] New sites added in 2007 and 2008


Figure 1. Lake Tahoe, CA-NV. Enclosed marina sites are shown in red.

limited our ability to snorkel some sites without generating excessive disturbance to the water column, thus onshore visual inspections were conducted as an alternative. Observation time in these sites ranged from 30-45 minutes in which presence and absence of warm-water non-native and native fish species were recorded. Boat electrofishing occurred at three of these sites; Tahoe Keys East, Tahoe Keys West, and Taylor Creek on May 26, Jun 15, Aug 22, and Oct 26, 2006. In 2007 electrofishing resumed on May 10, Jun 12, Aug 7, Oct 26, and Dec 3. In 2007 (except June) and 2008, low lake water level prevented access to Taylor Creek by boat, therefore only Tahoe Keys East and West were surveyed by electrofishing on May 14, July 17, and Sept 29.

Tahoe Keys is an extensive housing project and inland marina on the south shore constructed in the mid-1960's on the Upper Truckee Marsh. The Upper Truckee River once flowed through Tahoe Keys, but was diverted to prevent flooding. Tahoe Keys consists of an inland marina on the northeast portion of the project whose waters are separate from a residential area with boating channels and waterways for residents. In this report they are referred to as Tahoe Keys East and Tahoe Keys West respectively (Figure 2). One boating channel each for the marina and the homeowner section of Tahoe Keys is the only site for surface water exchange with the main body of the lake. The shallow backwaters contain abundant aquatic vegetation including non-native Eurasian water milfoil (*Myriophyllum spicatum*). Up to $150,000 in operating costs have been spent annually to control milfoil growth by mechanical harvesters (Eiswerth 2000). Warmer, lentic waters with abundant vegetation provides habitat for warm-water non-native fishes including: largemouth bass, bluegill, black crappie (*Pomoxis nigromaculatus)*, brown bullhead (*Ameiurus nebulosus)*, and goldfish (*Carassius auratus)*.

Taylor Creek originates at Fallen Leaf Lake. The outflow sources adjacent wetlands before emptying into Lake Tahoe 4 km west of Tahoe Keys. These waters are shallow and inundated with terrestrial and aquatic vegetation including Eurasian water milfoil. Elevated water temperatures in warmer months at Tahoe Keys and Taylor Creek make these suitable areas for warm-water fish to live and reproduce.


Figure 2. Google Earth satellite image of the Tahoe Keys. Shocking locations are denoted. Two water bodies make up Tahoe Keys, the marina portion (Tahoe Keys East), which is kept separate from the homeowner portion (Tahoe Keys West).

*Snorkel Survey*

Tahoe Keys East and West, and Taylor Creek are considered marina or embayment sites (also referred to as enclosed). ‘Non-marina’ (exposed) sites are considered control habitats where non-native species are not expected. Non-marina sites are free of constructed walls or piers arranged in a manner that prohibits water exchange and mixing with the main lake, while marina/embayment sites contain these features or are naturally enclosed by a geographic feature that prevents water mixing (i.e. Taylor Creek). Marina/embayment sites were thought to contain warmer temperatures in the summer months that allow non-native warm water fishes to persist and spawn. Accessibility in several public marinas and private marinas was contingent upon careful, respectful interaction with owners and managers. In some cases access for snorkeling was not granted (Homewood, Logan Shoals marinas) and were not included in this study.

Bi-weekly surveys consisted of up to 45-minutes of snorkeling and onshore visual inspection. Areas with stand-alone piers were snorkeled along the length of the pier to the shoreline. During each survey, presence and absence of native fishes and warm-water non-native fishes were recorded. DS1921Z-F50 i-button thermistors (Embedded Data Systems) recorded water temperature within a meter of the surface every 3 hours at all survey sites.

*Electrofishing Survey*

Electrofishing surveys were conducted with California Department of Fish and Game (CDFG) staff and equipment. Fish collections were quantified by timed electrical discharge to the water. Shock time was complete when the site appeared to be exhausted of fish. For Taylor Creek this required a shock time of no more than 35 minutes for all months. Tahoe Keys East was shocked an average of 25.6 minutes, and Tahoe Keys West an average of 32 minutes for all months. Lengths and weights of native fishes were taken on site when possible and then released. Warm-water non-native species were euthanized and processed in the lab the next day. Length, weight, and sex were recorded. Stomach contents were removed and preserved in 70% ethanol for later analysis. Dorso-lateral scales were removed from the left side of each fish and stored in a coin envelope for aging. In 2008, otoliths were also extracted and stored for corroboration of age determination (data not presented due to lack of time for laboratory analysis) and have been archived at the University of Nevada, Reno's Aquatic Ecosystems Analysis Laboratory.

*Diet analysis*

A total of 684 stomach contents were analyzed (394 bluegill, and 290 largemouth bass). Aquatic and terrestrial invertebrates were sorted to taxonomic order; fish and plants were identified to species when possible. All diet items were dried in a vacuum oven for 24 hours at 90 °C and weighed on a microbalance. "Proportion of diet" for each diet item in a stomach was calculated as the summed weight of each individual diet item divided by total weight of all diet items for that fish. Groups of size classes were established and average proportions for each size class were reported. Bluegill were separated into size classes with 4 cm intervals from 0.1 to 16.0 cm total length with the largest class >16.1 cm. Largemouth bass were separated into size classes with 4 cm intervals from 0 to 24 cm after which intervals increased to capture appropriate sample size (24.1-30.0, 30.1-40.0, 40.1+).

*Ageing*

Ages were determined from scales sampled in May, Jun, Oct 2006, and May, Jun 2007. Bluegill scales from 2006 and 2007, and largemouth bass scales from 2007 were prepared by dipping in boiling water, wiping with a cloth between the fingers, and mounting on microscope slides bound with clear tape. Ageing occurred independently by two observers. A photo was taken of each scale to be measured using a Nikon DS-U2 microscope camera (Technical Instruments). Scale radius and annuli lengths from the focus to the annulus were measured with NIS-D Elements: Documentation software (Technical Instruments).

*Movement tracking*

We captured largemouth bass and bluegill from the east section of Tahoe Keys Marina in a vegetated cove called the Sailing Lagoon. We anesthetized fish with clove oil and made a 1 cm incision into the ventral side of the fish, anterior to the pelvic girdle. A VEMCO acoustic transmitter (V7 for bluegill or V9 for largemouth bass) was implanted into the peritoneal cavity of each captured fish. The incision was closed with two number 4 gut sutures. Each transmitter tag contains an acoustic transducer and a microprocessor that controls the width of emitted signals ("pings") as well as the interval between pings during acoustic transmission (VEMCO 2006). The V9 transmitter tags are also equipped with a pressure sensor that did not function for this project.

The acoustic transmitters (pingers) use a single frequency (69 kHz) coding scheme called R64K. The pinger sends a train of acoustic pulses that are infrequent and random around an average delay (Table 4). This pulse train includes an ID number specific to each tag which permits identification of different individual fish (www.vemco.com, 2009). When fish carrying the acoustic transmitter swim within the range of the receivers (up to 122 m in Lake Tahoe, tested by coauthor Brant Allen), they are detected and recorded in the receiver. Detection data containing fish ID, date, and time were downloaded from the receivers five times throughout our sampling season in 2008 (June 24, July 9, July 25, October 23, and December 3).

Eight VEMCO VR2W receivers were placed within and around Tahoe Keys Marina area covering both the east and west section of the Marina (Figure 3 and Table 3). One receiver was place in Taylor Creek (west of Tahoe Keys) to track potential movement of largemouth bass and bluegill if they were to move out of Tahoe Keys. DS1921Z-F50 i-button thermistors (Embedded Data Systems) were attached to the receivers on July 25, 2008 to record daily water temperature at 3 hours interval.

Thirteen largemouth bass, total length ranging from 28 -38 cm, and three bluegill, total length ranging from 17- 18 cm, were tagged and released back into Sailing Lagoon on May 14th, 2008 (Table 2). Another largemouth bass and four bluegill were tagged and released at the same location on June 24, 2008 (Table 2). The fish were tracked from mid- May to early December 2008.

Table 2. Specification of the acoustic transmitter (Vemco V7 and V9) used in this study. Information was provided by VEMCO (www.vemco.com)

| Transmitter Tag | Sensor | Diameter (mm) | Frequency (kHz) | Length (mm) and Weight (g) | Transmit Interval (sec) | Battery life (days) |
|---|---|---|---|---|---|---|
| V7 | None | 7 | 69 | 18-22.5/0.7-1 | 150-300 | 200 |
| V9 | Pressure (100 m) | 9 | 69 | 21-46/1.6-3.5 | 50-150 | 400 |


Figure 3. Locations of the eight hydroacoustic receivers placed within and around Tahoe Keys Marina area covering the east and west section of the Marina. One other receiver (not shown in the figure above) was placed in Taylor Creek (West of Tahoe Keys

Marina) and was found to be missing on August 7, 2008. All receivers in the east section of the Marina were deployed on either May 12 or 27, 2008. The receiver placed at the outer west channel of the Marina was deployed on June 24, 2008.

Table 3. GPS coordinates and deployment and retrieval dates of hydroacoustic receivers placed within and around Tahoe Keys Marina area.

| Site name | Serial number of receiver | Deployme nt date | Retrieval date | GPS coordinate |
|---|---|---|---|---|
| Outermost green buoy | 102110 | 5/27/2008 | 12/03/2008 | n/a |
| Taylor Creek | 102112 | 5/27/2008 | Missing | N38 56.517; W120 03.380 |
| Outer west channel | 102114 | 6/24/2008 | 10/23/2008 | n/a |
| Inner east channel | 102116 | 5/13/2008 | 12/03/2008 | N38.93868; W120.00459 |
| Gas dock | 102118 | 5/13/2008 | 12/03/2008 | N38.93481; W120.00331 |
| Marina Cove | 102119 | 5/13/2008 | 12/03/2008 | N38.93358; W12000243 |
| 3rd red buoy | 102120 | 5/27/2008 | 12/03/2008 | N38 56.400; W120 00.452 |
| Sailing Lagoon | 102121 | 5/13/2008 | 10/23/2008 | N38.93866; W120.00319 |
| Outer east channel | 102122 | 5/13/2008 | 12/03/2008 | N38.93955; W120.00569 |

Table 4. Size and acoustic transmitter information of the tagged fish used in this study.

*Largemouth bass*

| Pinger tag | Total length (cm) | Weight (g) | Date deployed |
|---|---|---|---|
| 13002 | 31.2 | 433.8 | 05/14/08 |
| 13003 | 28.7 | 442.6 | 05/14/08 |
| 13004 | 29 | 361 | 05/14/08 |
| 13005 | 36.8 | 642 | 05/14/08 |
| 13006 | 35.6 | 750.8 | 05/14/08 |
| 13007 | 31.8 | 526.8 | 05/14/08 |
| 13008 | 31.8 | 486.1 | 05/14/08 |
| 13009 | 33 | 442.4 | 05/14/08 |
| 13010 | 38.2 | 800 | 05/14/08 |
| 13011 | 36.8 | 922 | 05/14/08 |
| 13012 | 36.8 | 737 | 05/14/08 |
| 13013 | 34.3 | 598 | 05/14/08 |
| 13014 | 30.5 | 360 | 05/14/08 |
| 13017 | 36.5 | 864 | 06/24/08 |

*Bluegill*

| Pinger tag | Total length (cm) | Weight (g) | Date deployed |
|---|---|---|---|
| 7609 | 17 | 108 | 05/14/08 |
| 7610 | 16.9 | 95.6 | 05/14/08 |
| 7611 | 17.9 | 97 | 05/14/08 |
| 7612 | 17.7 | 76.9 | 06/24/08 |
| 7613 | 18 | 123.3 | 06/24/08 |
| 7615 | 15.5 | 67.3 | 06/24/08 |
| 7616 | 18.5 | 138.32 | 06/24/08 |

*Surface Water Temperature modeling*

Data from temperature probes deployed in 2003 and 2006 were used to record the variability in daily surface water temperature among inshore and offshore locations around the lake. Cluster analysis and visual inspection of graphical outputs were used to identify thermally similar sites and to classify regions that were thermally distinct (i.e. warmer and cooler groups) (See Results - *SWT model: Cluster analysis*). Our modeling effort focused on both the coolest (exposed) and the warmest (enclosed) sites to capture the entire range of thermal variability observed in Lake Tahoe.

*1. Base model development*

First, a base model which characterizes the SWT of exposed sites (OEI) was developed. We used the empirical approach developed by Matuszek and Shuter (1996) to structure our base model. This model is a function of 5-day and 20-day running averages of air temperatures (ATemp), and Julian day (yday). We calibrated the model with 7 years (1996-2003) of biweekly temperature data, and arrived at the following equation:

$$SWT_{OEI} = -20.6783 + 0.16255(ATemp5) + 0.29978(ATemp20) + 0.26121(yday) - 5.37\mathrm{E}^{-4}(yday)^2$$

The accuracy of the base model was validated using 1 year of daily water temperature (2006) and 29 years of monthly point data (1967-1995) from independent data sets.  The predicted water temperature for 2006 using the base model compared with the observed water temperature (RMSE= 0.89 and mean residual = 0.657) are shown (Figure 4). Individual residual values (observed water temperature – predicted water temperature), grouped by month, across 29 years of observed water temperatures are shown (Figure 5). The annual root mean square errors (RMSE) for these residuals ranged from 0.73 to 1.87 (median, 0.98) and the overall bias was low (mean residual: 0.0482). In addition, 84.9 % of all projected temperatures ($N$ = 569) were within +/-1.5 °C of their respective observed water temperatures.

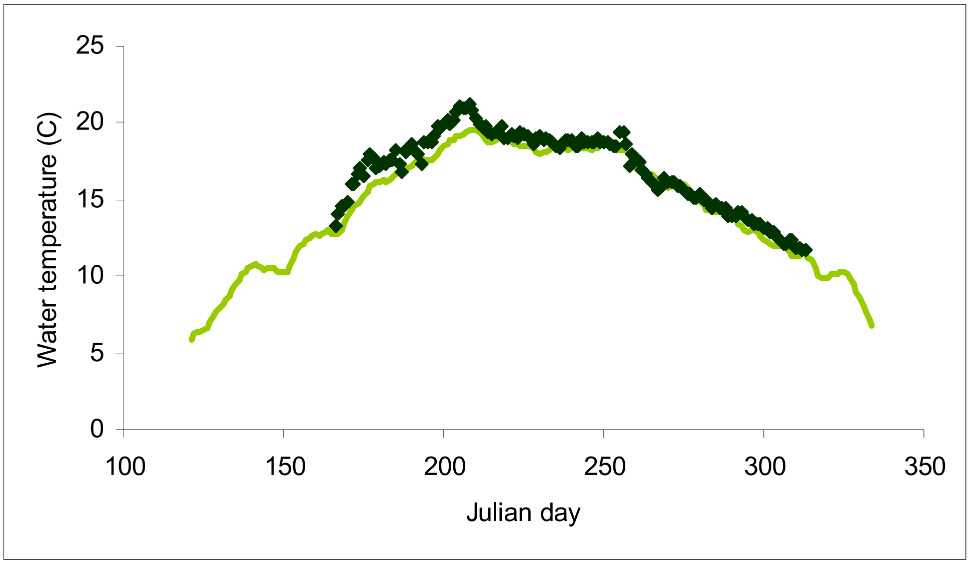


Figure 4. Predicted (solid line) and observed (diamonds) surface water temperature (SWT; °C) for exposed sites in 2006. Predicted SWT were generated using the exposed-sites base model.

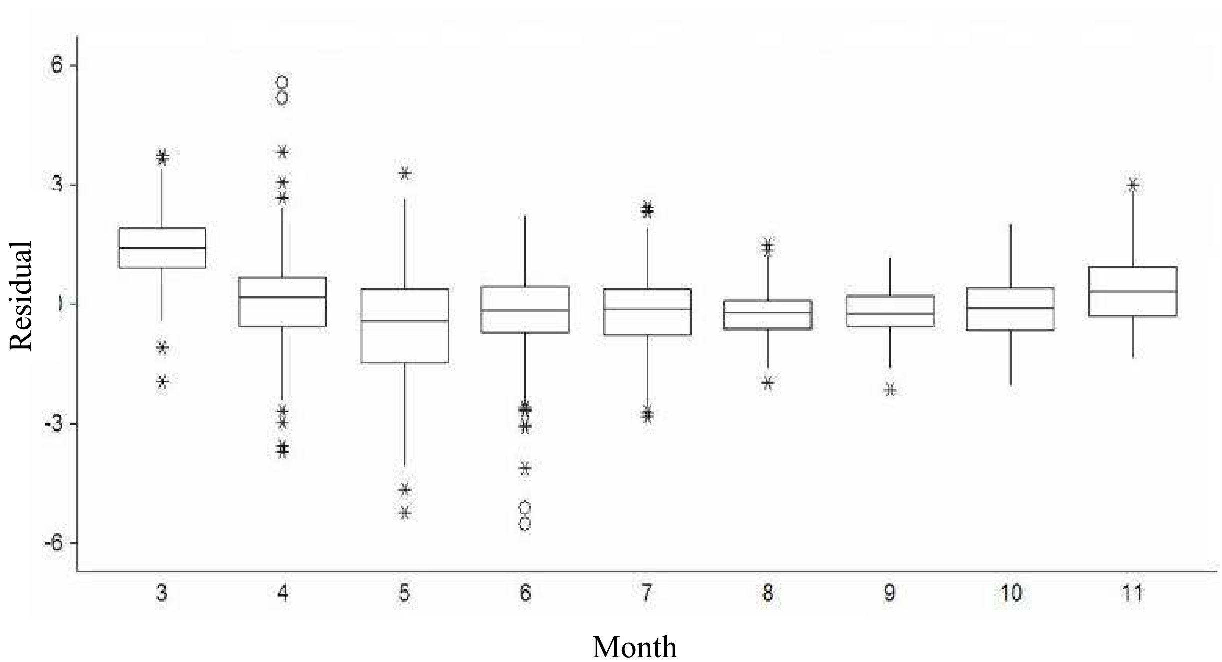


Figure 5. Comparison of observed and predicted SWT [residuals = (observed-predicted)] for the exposed sites, grouped by month. Observed SWT were collected between 1967 and 1995. Predicted values were generated using the exposed-sites base model.

*2. Supplementary model development*

An additional supplementary model was developed to generate SWT predictions for enclosed sites (TK). Based on the correlation between the SWT of the exposed and the enclosed sites, we constructed a biphasic model which breaks down the correlation into a warming period and a cooling period. The model generates SWT projections for the enclosed sites by using the result from the base model for the exposed sites. The hottest day (HTD) in terms of SWT at the enclosed sites was used as the divider for the biphasic model.

$$SWT_{TK(warming)} = 0.8946 \cdot SWT_{OEI(all\ yday \leq HTD)} + 5.6391$$

$$SWT_{TK(cooling)} = 1.7252 \cdot SWT_{OEI(all\ yday \geq HTD)} - 12.5718$$

*MODIS satellite temperature data: Predicting nearshore temperatures at many locations*

Previous limnological monitoring in Lake Tahoe has focused on the pelagic environment with limited information available in the nearshore or benthic environments (Chandra et al. 2005). Thus, there is limited nearshore temperature data. In order to model nearshore temperatures over the bass growing season, offshore temperatures derived by MODIS (Moderate Resolution Imaging Spectroradiometer; Figure 6) satellite imagery were used in conjunction with nearshore temperatures recorded in the field by automated i-button thermistors®. These data were used to model nearshore-offshore temperature relationships that predicted nearshore temperatures at finer resolution.

As part of NASA's Earth Observing System (EOS), MODIS reads Lake Tahoe surface water temperature twice daily at 1 $km^2$ spatial resolution with 0.5 ˚C accuracy.

However, MODIS cannot measure nearshore temperatures (within 1 km) accurately because the readings are contaminated by land temperature; thus MODIS temperatures were recorded 1300 m from shore. In ArcGIS, offshore sites were selected to measure temperature by MODIS at 2 km intervals on a transect parallel to the shoreline (Figure 7). Daily offshore temperatures were extracted at geolocations of the resulting 49 offshore MODIS sites from the Land Processes Distributed Active Archive Center (LP DAAC). Spectral tests identified and removed artificially cold measurements caused by cloud interference. Weekly average temperatures were then calculated at the 49 offshore sites from May to October 2006.

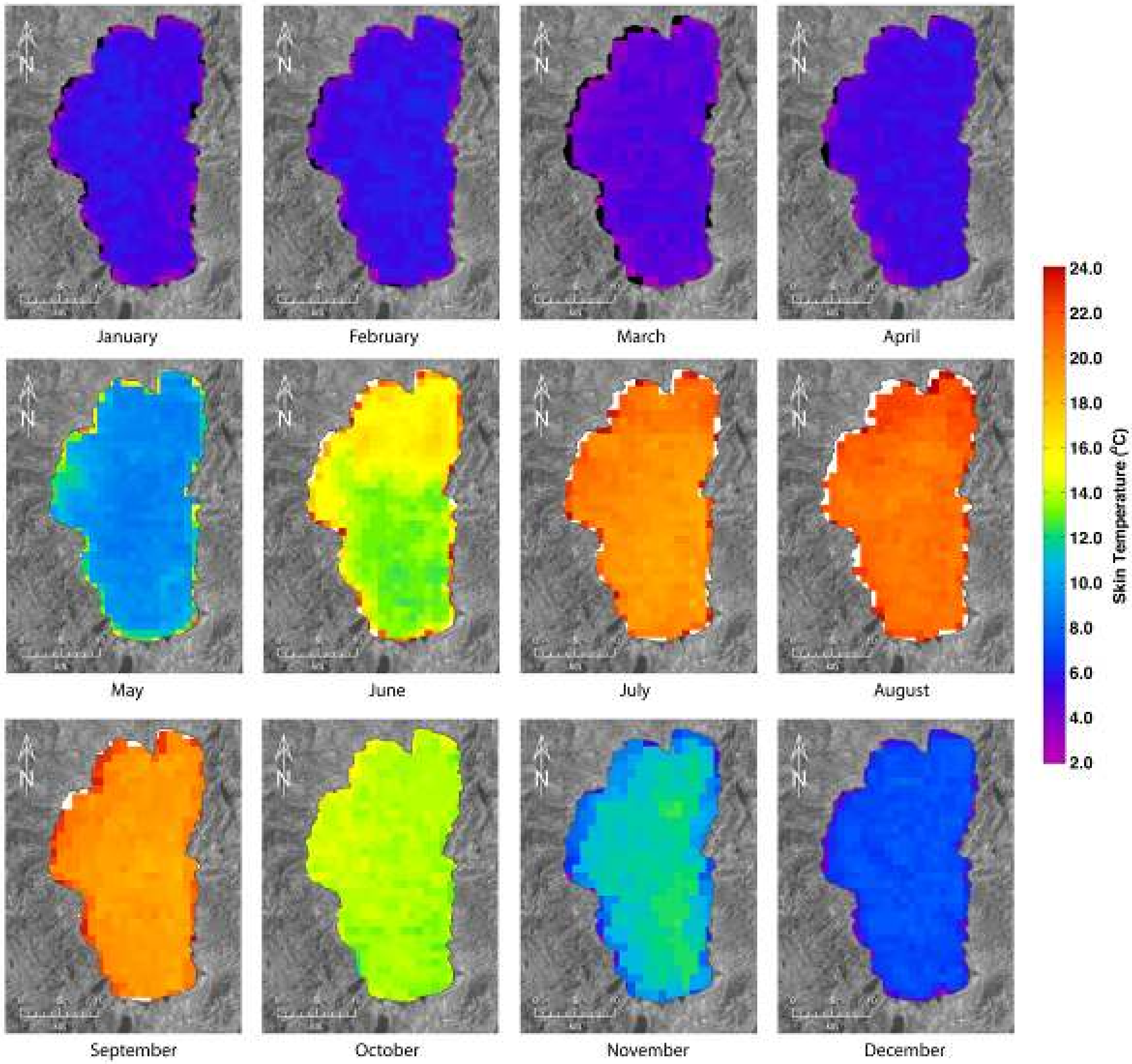


Figure 6. MODIS-derived water temperatures on a cloudless day for each month during 2006. Lake-wide temperature is shown at a pixel resolution of 1 km$^2$. Provided by Todd Streissberg, UC Davis.

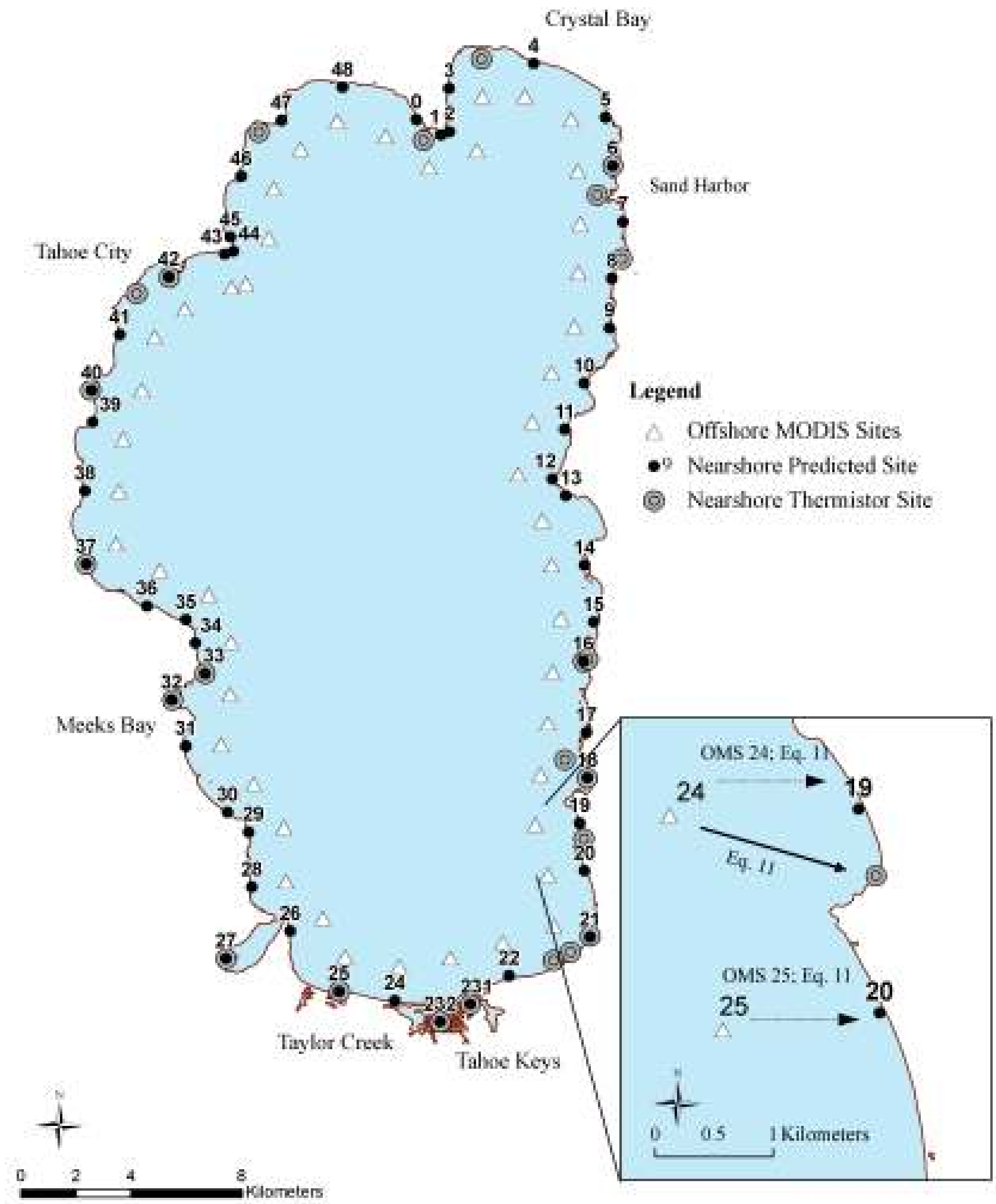


Figure 7. Weekly temperatures were predicted at 50 nearshore sites (●) in Lake Tahoe, using 20 regression equations between satellite and field data. Nearshore temperatures measured by thermistors (◎) were regressed against the nearest offshore MODIS site (△). The inset figure illustrates the regression of thermistor data against an offshore MODIS site, No. 24 (solid black arrow; Nearshore temperature = 0.7854 * Offshore temperature + 4.49; $R^2$=0.97). The resulting regression equation, no. 11, estimated temperatures at all nearshore sites nearest to the thermistor. Temperatures were estimated at nearshore sites 19 and 20 (dashed arrows) using equation 11, and temperatures from the paired offshore MODIS site.

Nearshore epilimnetic temperatures (1-2 m deep) were recorded in the field by thermistors at 20 nearshore sites (see above). Weekly mean temperatures were calculated from thermistors for May to October 2006. These nearshore thermistor temperatures were then regressed against offshore temperatures from the nearest offshore MODIS site.

A regression was derived for each of the 20 thermistor datasets, and were used to estimate temperatures at 50 nearshore sites. The 50 nearshore sites were also selected in ArcGIS and paired with the 49 offshore sites. One additional nearshore site was added in Emerald Bay and paired to the offshore MODIS site adjacent to the bay, but in the main part of the lake. There was no coinciding offshore MODIS site within Emerald Bay because MODIS resolution is limited to 1 $km^2$. At each of the nearshore sites temperatures were modeled using the nearest of the 20 regression equations, as determined by which thermistor site was nearest to the nearshore site being modeled. Geographical features known to affect epilimnetic temperatures were also used to guide which regression equation was assigned to a nearshore site (Steissberg et al. 2005). Offshore MODIS temperatures from the paired site were input to the assigned regression equation to estimate weekly temperatures at each of the 50 nearshore geolocations at ~2 km intervals along the shoreline (Figure 7). The temperature estimates were used to calculate suitable spawning locations.

*Predicting bass establishment in noninvaded locations: Model overview*

Given the relatively recent introduction of warmwater non-native fishes coupled with climate-induced lake warming, a model was developed for one of these warmwater fishes, the largemouth bass, to predict where establishment is likely and what the potential impacts of bass predation on native fishes will be. The model for bass establishment consisted of two nearshore layers, 1) thermally suitable spawning locations and 2) areas with adequate structure (submerged aquatic vegetation). Distribution, and consequently establishment, of warmwater species is often limited by length of the growing season (Rahel 2002), followed by spawning and recruitment capability (Post et al. 1998). Given that Lake Tahoe's littoral zone is already thermally suitable for bass growth (Ngai 2008), nearshore temperature estimates were used to measure thermal suitability for spawning potential to parameterize layer 1. Distribution of submerged aquatic vegetation created layer 2. Layers (1) and (2) were combined to classify each site as either highly likely, likely, or least likely to exhibit bass establishment given current conditions (Figure 8). Classifications for bass establishment were driven by the following assumptions: bass physiology is governed by temperature such that bass will seek temperatures nearest to their thermal optimum (Magnuson et al. 1979; Rice et al. 1983), successful spawning will increase establishment likelihood, and bass commonly occupy vegetated habitats (Carlander 1975; Shirley and Andrews 1977; Savino and Stein 1982).

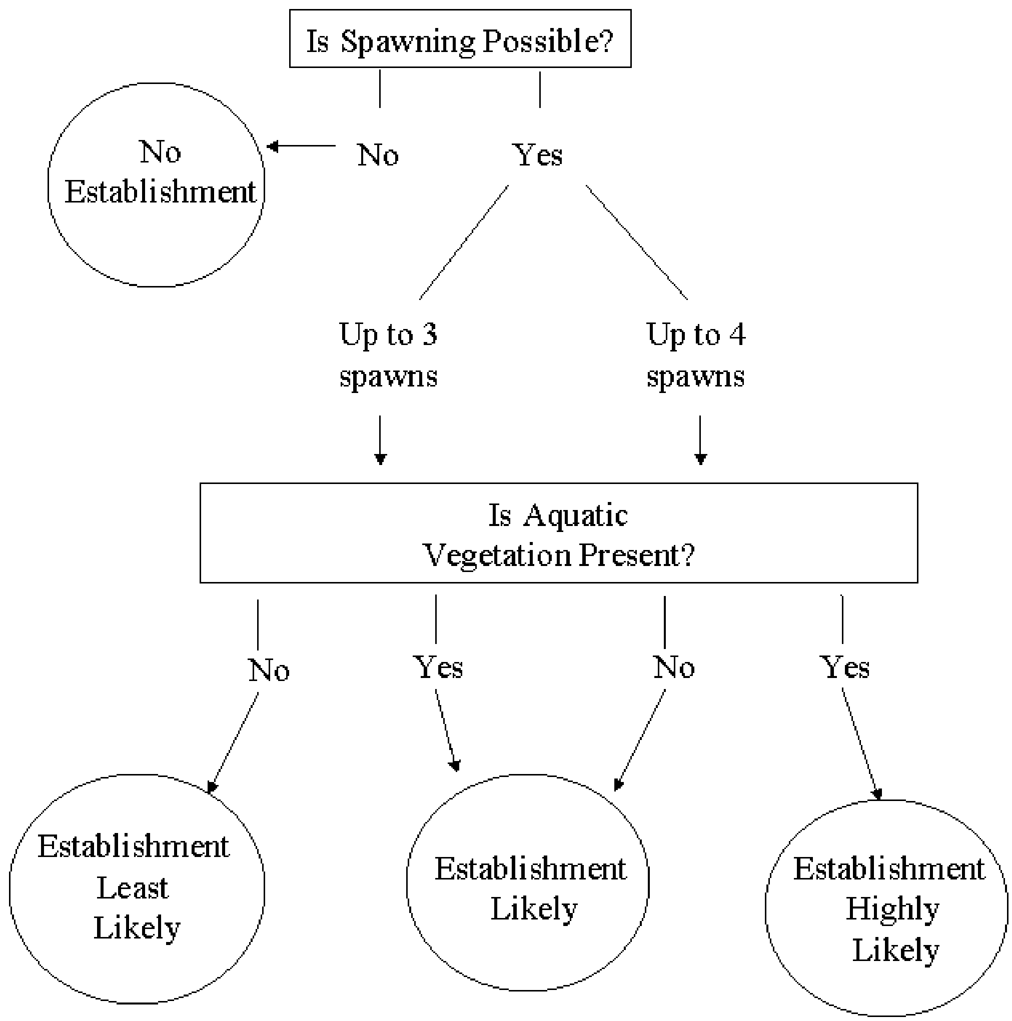


Figure 8. Diagram of decision pathway to classify likelihood of bass establishment in Lake Tahoe. Items in rectangles are model layers, with their outcomes underneath them, and the resulting classifications for bass establishment are circled.

After establishment likelihood classification was performed, a bioenergetics model estimated consumption to simulate predation pressure on nearshore fish communities. Consumption was estimated by Fish bioenergetics 3.0 (Hanson et al. 1997), which uses a mass-balance energy equation to calculate consumption given growth inputs by the user, and estimated losses to metabolism and excretion that rely on user input temperatures, fish weight, and physiological parameters. A bioenergetics model for consumption models was first constructed for bass in Tahoe Keys using bass growth and diets observed in the Tahoe Keys population. This Tahoe Keys model for consumption was used as the base consumption model that was applied to all other nearshore sites by keeping all data inputs the same, except temperature, which varied at each site modeled. Thus consumption was estimated at several nearshore sites and formed a third layer of data, 3) consumption by bass, which examined the range, magnitude, and intra-lake variability of consumption by bass. Total consumption by bass at two different densities, over the growing season was compared to historical nearshore fish biomass estimates. It was assumed predation impacts would be greatest where bass could have eliminated nearshore biomass by consuming an amount that was $\geq 100$ % of nearshore fish biomass recorded at a particular site.

*Suitable Spawning Locations (Layer 1)*

Thus, to identify suitable spawning locations, Layer 1 was parameterized with the number of potential spawns possible at each of the 50 nearshore sites. Largemouth bass begin spawning when temperatures reach 15.9 ˚C (Kramer and Smith 1960). Nest building to swim up takes 16 d, and up to 21 d can pass between spawns (Keast and Eadie 1984; J. Powell pers. comm.). From nearshore temperature estimates the potential number of spawns was calculated as total degree days ≥15.9 ˚C, divided by 37 d (16 d + 21 d).

*Habitat (Layer 2)*

Submerged aquatic vegetation is the primary habitat for bass in north-temperate lakes. Vegetation provides cover for juveniles, and protects nests from wave action (Savino and Stein 1982). Assuming bass in Lake Tahoe prefer vegetated areas, as they do in other large natural lakes (Carlander 1975); vegetation observations from this study were combined with previous aquatic plant surveys (Anderson 2006) to attribute the habitat layer. Presence/absence of aquatic vegetation was recorded during bi-weekly snorkel surveys at 21 locations from May to October 2006 (Kamerath et al. 2008). In the habitat layer, a nearshore site was vegetated if vegetation was present within the sites boundary. Site boundaries were determined by extrapolation methods described below in 'Data Extrapolation and Layer Construction.' The habitat layer was overlaid with the 'suitable-spawning' layer to identify sites where bass establishment was likely.

*Consumption by Bass (Layer 3)*

Consumption by bass was estimated at 50 nearshore sites to simulate predation pressure on native fishes. Consumption was estimated using Fish Bioenergetics 3.0, also known as the Wisconsin Model (Hanson et al. 1997). The base consumption model was applied to nearshore locations outside of Tahoe Keys by keeping all inputs and parameters the same, excluding temperature inputs which were specific for each site modeled.

The Wisconsin model uses a mass balance energy equation to calculate either consumption or growth on the tenet that growth is proportional to the net energy consumed by a fish [i.e. Growth = Consumption – (Metabolism + Excretion)]. In this application we provide growth data and solve for consumption (C) of an individual fish,

$$C = (\Delta B + G) + (R + A + S) + F + U$$

where C equals the sum of physiological processes: somatic ($\Delta B$) and gonadal growth (G), respiration (R), active metabolism (A), specific dynamic action (S), egestion (F), and excretion (U). Growth is assumed from start and end weights provided by the user. Start and end weights were measured from Tahoe Keys bass in May and October. Metabolism terms (R, A, S) are modeled as a function of Tahoe Keys temperature regime, daily interpolations of fish weight, and an activity multiplier. Egestion (F), excretion (U), and metabolism (R, A, S) are calculated as constant proportions of consumption.

A proportionality constant, P, is estimated by the model, and ranges from 0.0 to 1.0. P represents the proportion of maximum consumption at which a fish is feeding, as governed by user inputs of temperature and fish weight. Thus if $P = 0.30$ a fish is consuming at 30 % of its maximum allowable consumption. Consumption rate is calculated as a function of the estimated P, maximum allowable consumption, and a temperature dependence function. (Hewett and Johnson 1992; Hanson et al. 1997).

Consumption in the Tahoe Keys, the primary location currently containing bass in the lake, was modeled from May to October 2006 (growing season) for 8 bass cohorts aged 1 to 8 years (Kamerath et al 2008). It was assumed this model period represented total annual consumption because bass feeding and growth is negligible at temperatures < 10 $^{\circ}$C and may be limited by photoperiod in fall months (Johnson and Charlton 1960; Carlander 1975; Coutant 1975). Fish were assigned to a cohort based on age-length regressions derived from scale ages (Bagenal 1978). Start and end weights were estimated from age-length regressions and length-weight regressions (Table 5). Diets for each cohort were obtained by electrofish sampling the Tahoe Keys for bass in May, June, August, and October 2006 (Kamerath et al. 2008). Diet items from bass stomachs were sorted to Order, dried in an 89 °C drying oven for 24 hours, and weighed. The Wisconsin model requires wet weight inputs, so dry weights of diet items were converted assuming they weighed 15 % of total wet weight (Cummins and Wuycheck 1971; Wetzel 2001). Diet proportions by weight were calculated and input in the model for each cohort in May, June, August, and October (Table 6). Physiological parameters and prey energy densities required by the model were taken from literature (Cummins and Wuycheck 1971; Rice et al. 1983; Hanson et al. 1997; Ruzycki and Beauchamp 1997), and are shown in Table 7 and Table 8 respectively. The temperature inputs for the Tahoe Keys base model were the weekly average temperatures from the Tahoe Keys nearshore site (Site No. 23a) (Table 9). These temperatures were derived using the methods described in the 'Nearshore Temperature' section.

Table 5. Length and weight for largemouth bass of cohorts (age classes) 1 to 8 from Tahoe Keys in 2006. Start and end weights were inputs to the Wisconsin Model. *Cohort not caught; these values extrapolated from age-length regression curves. To obtain weights, mean length at age was first estimated from age-length linear regression ($TL_{cm}$ = 3.83·Cohort + 9.85; $r^2$ =0.62). Mean weight per age was then estimated using log-linear length-weight regression (Log Weight = 3.21·Log TL -2.10; $r^2$ =0.99).

| **Bass Cohort** | **TL (cm)** | **Start (May) Weight (g)** | **End (Oct) Weight (g)** |
|---|---|---|---|
| 1* | 13.68 | 35.57 | 78.67 |
| 2 | 17.52 | 78.67 | 148.62 |
| 3 | 21.35 | 148.62 | 252.70 |
| 4 | 25.18 | 252.70 | 398.48 |
| 5 | 29.01 | 398.48 | 593.78 |
| 6 | 32.85 | 593.78 | 846.65 |
| 7* | 36.68 | 846.65 | 1165.34 |
| 8 | 40.51 | 1165.34 | 1558.29 |

Table 6. Bass diet proportions from Tahoe Keys. If cohort was not caught each month, diets of neighboring cohorts were averaged..

| Month | Cohort | Zooplankton | Fish | Plant | Aquatic Invertebrates | Terrestrial Invertebrates | Diptera | Ephemeroptera | Mollusca | Amphipod | Decapoda |
|---|---|---|---|---|---|---|---|---|---|---|---|
| May | 1 | 0.072 | 0.675 | 0.001 | 0.098 | 0.001 | 0.104 | 0.022 | 0.011 | 0.016 | 0 |
| | 2 | 0 | 0.999 | 0 | 0 | 0 | 0.001 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | 0 | 0.598 | 0 | 0.017 | 0 | 0 | 0 | 0 | 0 | 0.385 |
| | 5 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 6 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 7 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 8 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Jun | 1 | 0.014 | 0 | 0.004 | 0.264 | 0.006 | 0.094 | 0.612 | 0.001 | 0.004 | 0.001 |
| | 2 | 0 | 0.600 | 0 | 0.015 | 0.006 | 0.004 | 0 | 0 | 0 | 0.374 |
| | 3 | 0 | 0.500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.500 |
| | 4 | 0 | 0.750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.250 |
| | 5 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 6 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 7 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 8 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aug | 1 | 0.013 | 0.229 | 0 | 0.315 | 0.050 | 0.041 | 0.002 | 0.002 | 0.015 | 0.334 |
| | 2 | 0 | 0.201 | 0 | 0.030 | 0.013 | 0.008 | 0 | 0 | 0 | 0.749 |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.000 |
| | 4 | 0 | 0.500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.500 |
| | 5 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 6 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 7 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 8 | 0 | 0.999 | 0 | 0 | 0 | 0 | 0 | 0.001 | 0 | 0 |
| Oct | 1 | 0.016 | 0.965 | 0 | 0.002 | 0 | 0.012 | 0 | 0 | 0.005 | 0 |
| | 2 | 0 | 0.408 | 0 | 0.053 | 0.034 | 0 | 0 | 0 | 0 | 0.504 |
| | 3 | 0 | 0.644 | 0 | 0.016 | 0 | 0 | 0 | 0 | 0 | 0.340 |
| | 4 | 0 | 0.822 | 0 | 0.008 | 0 | 0 | 0 | 0 | 0 | 0.170 |
| | 5 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 6 | 0 | 0.500 | 0.500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 7 | 0 | 0.500 | 0.500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 8 | 0 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 7. Value and description of largemouth bass physiological parameters input in the Wisonconsin model. Parameters developed by Rice et al. 1983.

| Parameter | Unit | Value | Description |
|---|---|---|---|
| Consumption | | | |
| CA | $g \cdot g^{-1} \cdot d^{-1}$ | 0.33 | Intercept of the mass dependence function of consumption |
| CB | $g \cdot g^{-1} \cdot d^{-1}$ | -0.325 | Mass dependence coefficient of consumption |
| CQ | n/a | 2.65 | Temperature dependence coefficient of consumption |
| CTO | °C | 27.5 | Temperature at which consumption is 0.98 of the maximum consumption rate |
| CTM | °C | 37 | Maximum temperature above which consumption ceases |
| Respiration | | | |
| RA | $g \cdot g^{-1} \cdot d^{-1}$ | 0.00279 | Grams of $0_2$ consumed by a 1 g fish at RTO |
| RB | n/a | -0.355 | Slope of the allometric mass function for standard metabolism |
| RQ | $°C^{-1}$ | 0.0811 | Rate at which the function increases over relatively low water temperatures (approximates Q10) |
| RTO | °C | 0.0196 | Optimum temperature for respiration (where respiration is highest) |
| RTM | °C | 0 | Maximum water temperature for respiration |
| RTL | °C | 0 | Lethal water temperature for respiration |
| RK1 | $cm \cdot s^{-1}$ | 1 | Intercept for swimming speed above cutoff temperature |
| RK4 | $°C^{-1}$ | 0 | Mass dependence coefficient for swimming speed at all water temperatures |
| ACT | $cm \cdot s^{-1}$ | 1 | Activity multiplier ("Winberg multiplier") |
| BACT | $cm \cdot s^{-1}$ | 0 | Water temperature dependence coefficient of swimming speed below RTL |
| SDA | "%" | 0.163 | Constant fraction of assimilated energy (consumption minus egestion) |
| Egestion/Excretion | | | |
| FA (fecal) | "%" | 0.104 | Constant fraction of consumption |
| UA (nitrogen) | "%" | 0.068 | Constant fraction of assimilated energy |

Table 8. Energy densities of prey items in bass diet. Values were input to the Wisconsin Bioenergetics model.

| Diet Item | Energy Density (Joules·$g^{-1}$ wet weight) | Reference |
|---|---|---|
| Plant | 2418 | Cummins and Wuycheck 1971 |
| Zooplankton | 3860 | Leuke and Brandt 1993 |
| Aquatic invertebrates | 3175 | Cummins and Wuycheck 1971 |
| Diptera | 2564 | Cummins and Wuycheck 1971 |
| Ephemeroptera | 3431 | Cummins and Wuycheck 1971 |
| Mollusca | 1799 | Cummins and Wuycheck 1971 |
| Amphipod | 3907 | Cummins and Wuycheck 1971 |
| Fish | 5607 | Ruzycki and Beauchamp 1997 |
| Decapoda | 2159 | Cummins and Wuycheck 1971 |
| Terrestrial invertebrates | 3421 | Cummins and Wuycheck 1971 |

Table 9. Temperature inputs to the Tahoe Keys bass consumption model. The Tahoe Keys model corresponds to nearshore site 23a.

| Date | Day of simulation | Tahoe Keys Temperature (°C) |
|---|---|---|
| 5/25/2006 | 1 | 11.4 |
| 5/28/2006 | 4 | 13.9 |
| 6/4/2006 | 11 | 16.0 |
| 6/11/2006 | 18 | 16.1 |
| 6/18/2006 | 25 | 19.1 |
| 6/25/2006 | 32 | 19.3 |
| 7/2/2006 | 39 | 20.3 |
| 7/9/2006 | 46 | 20.4 |
| 7/16/2006 | 53 | 22.3 |
| 7/23/2006 | 60 | 23.2 |
| 7/30/2006 | 67 | 20.6 |
| 8/6/2006 | 74 | 20.9 |
| 8/13/2006 | 81 | 20.4 |
| 8/20/2006 | 88 | 20.5 |
| 8/27/2006 | 95 | 19.9 |
| 9/3/2006 | 102 | 20.2 |
| 9/10/2006 | 109 | 18.9 |
| 9/17/2006 | 116 | 17.0 |
| 9/24/2006 | 123 | 16.8 |
| 10/1/2006 | 130 | 15.5 |
| 10/8/2006 | 137 | 14.9 |
| 10/15/2006 | 144 | 14.4 |
| 10/22/2006 | 151 | 13.8 |
| 10/26/2006 | 155 | 13.8 |

Maintenance ration in the Tahoe Keys was calculated for all cohorts by iteratively adjusting the models proportionality constant, P, until no growth occurred over the model period, which was indicated by equivalent start and end weights. These values were compared to Tahoe Keys base model consumption rates. If a fish was feeding above its maintenance ration, positive growth is assumed to occur, and alternatively a fish feeding below its maintenance ration has negative growth.

The Tahoe Keys base model was applied to the remaining nearshore sites to estimate the magnitude and spatial variability of predation impacts nearshore. Temperature inputs varied for each site modeled because temperatures can vary in space and time. This assumes temperatures from each location would represent the thermal experience of a hypothetical bass. Furthermore, since we were modeling hypothetical populations, bass diets from the Tahoe Keys were assumed to be the same as bass diets at all sites modeled. Thus, temperature drove the variability in the model's consumption estimates for each nearshore site.

During the 2006 snorkel survey, bass were counted when present outside the Tahoe Keys, and divided by snorkel area to calculate minimum and maximum bass densities observed in the lake. Tahoe Keys bass density was determined by dividing the mean number of fish caught, from the four electroshock events, by sample area. Individual bass consumption estimates were then scaled up to minimum (2 bass$\cdot$ha$^{-1}$) and maximum (50 bass$\cdot$ha$^{-1}$) densities observed during 2006. Individual consumption rates of each cohort were multiplied by the frequency that cohort existed in the Tahoe Keys population, so that consumption was not over or under-represented for certain cohorts. Total biomass consumed, the sum of daily consumption for the entire model period (kg$\cdot$155 d$^{-1}$), by minimum and maximum bass densities attributed layer 3. The potential impacts of bass based on available biomass data of nearshore fishes, was calculated as the proportion of nearshore biomass consumed by bass ($P_{NB}$):

$$P_{NB} = \left(\frac{BC}{NB}\right) \cdot 100$$

where BC is biomass consumed ($kg \cdot ha^{-1}$) by bass densities, and NB is nearshore fish biomass ($kg \cdot ha^{-1}$) during the summer season (adapted from Beauchamp et al.1991).

Beauchamp et al. (1991) recorded fish counts in Lake Tahoe at 35 nearshore locations. Fish counts of adults and juveniles were converted to total weight from species-specific length-weight regressions (Beauchamp et al. 1991). Nearshore fish biomass was calculated as total fish weight observed at each transect divided by transect area (0.4 ha). NB was calculated as the sum of observations at 1, 3, and 10 m transects for April to September. NB was assumed to represent total summer biomass. $P_{NB}$ measures predation pressure of minimum (2 $bass \cdot ha^{-1}$) and maximum (50 $bass \cdot ha^{-1}$) densities at locations where Beauchamp et al.'s (1991) observations were contiguous with our nearshore sites. Where more than one nearshore biomass estimate occurred within a nearshore site, $P_{NB}$ was calculated using the highest NB observed within a site. This affords a conservative view of impacts by bass predation.

*Data Extrapolation and Layer Construction*

Data that populated the three layers were measured, observed, or modeled at 50 nearshore geolocations. Data were extrapolated using Thiessen polygons (ESRI, 1994) to create a 'layer', which was a continuous swath of data made up of 50 nearshore polygon areas. Each polygon area was attributed with data taken at the geolocation within the polygon. The extrapolation assumed temperature and bioenergetics data at a nearshore geolocation extended half the distance (~1 km on either side) to the next nearshore geolocation. Since nearshore site polygons were extrapolated to a continuous distance from shore, and bathymetry is irregular, some sites included profundal zone depths (>10 m) where bass are unlikely to occur in the growing season (Carlander 1975; Beauchamp et al. 1994). This is an artifact of extrapolation and any profundal zone areas that fall within a polygon should not be considered relevant for bass establishment, and thus monitoring activities should remain within the littoral zone.

## Results and Discussion

### *Distribution of warm-water non-native fishes*

Based on our observation, lake-wide establishment of warm-water non-native fishes including largemouth bass and bluegill have not yet occurred. Snorkeling surveys from all three years show that smaller satellite populations of bluegill and largemouth bass do exist outside of Tahoe Keys and Taylor Creek, however their distributions have declined since 2006 (Figure 9 and 10, respectively).

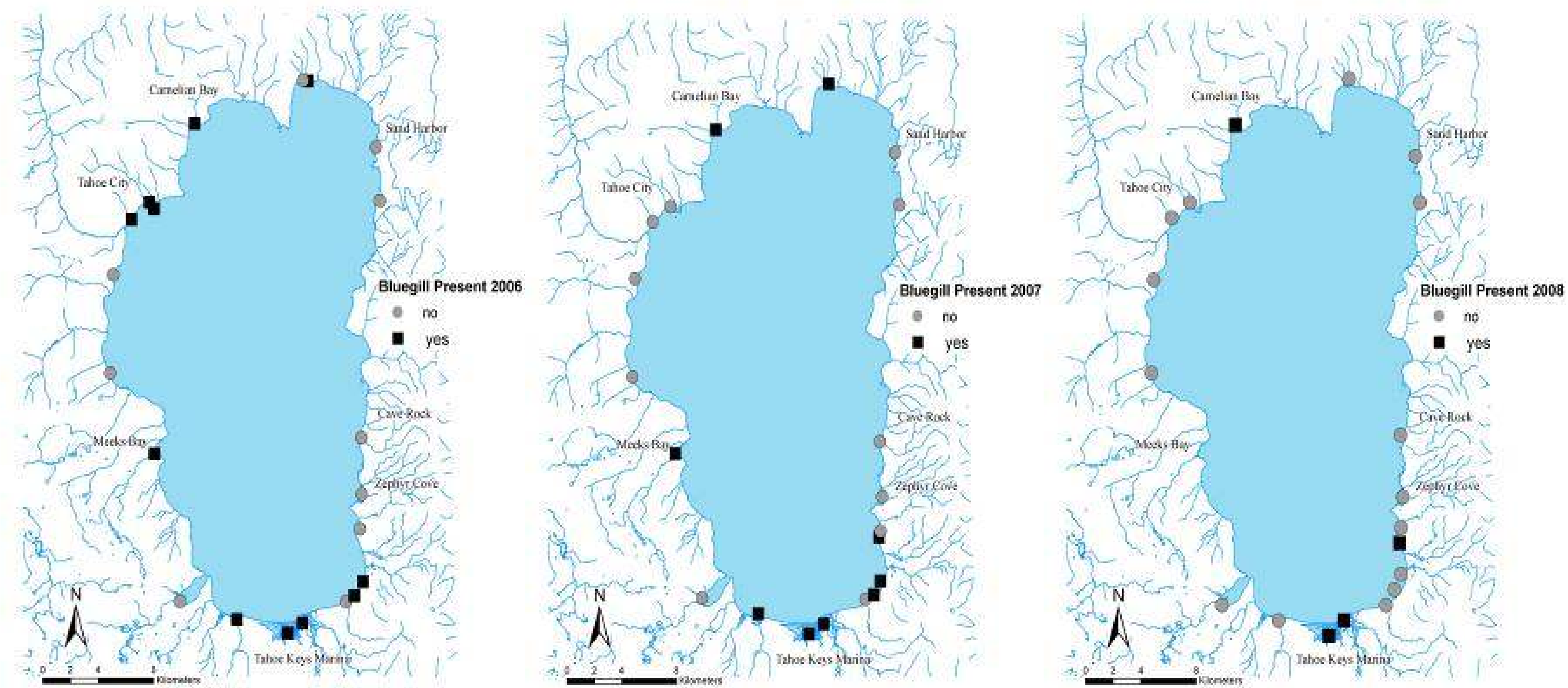


Figure 9. Presence (black squares) and absence (grey circles) of bluegill along Lake Tahoe's shoreline between 2006 and 2008. Bi-weekly snorkel surveys and onshore visual inspections were conducted from May to Nov. 52 % of sites in 2006, 45 % in 2007, and 21 % in 2008 were occupied by bluegill in at least one snorkel survey session during our sampling period.

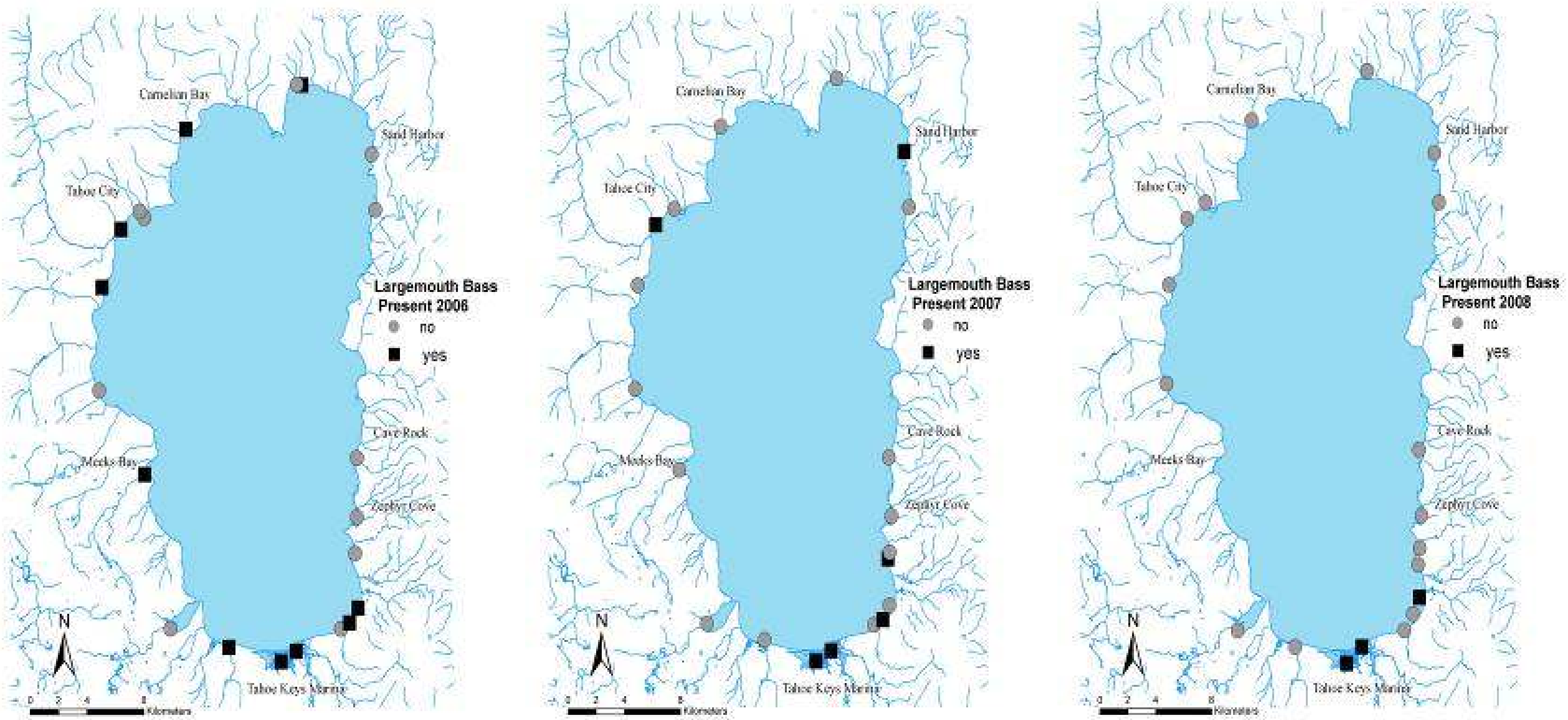


Figure 10. Presence (black squares) and absence (grey circles) of largemouth bass along Lake Tahoe's shoreline between 2006 and 2008. Bi-weekly snorkel surveys and onshore visual inspections were conducted from May to Nov. 48 % of sites in 2006, 30 % in 2007, and 16 % in 2008 were occupied by largemouth bass in at least one snorkel survey session during our sampling period.

*Catch*

In 2006, young-of-year and smaller size classes of largemouth bass and bluegill were most prevalent between June and August shocking events (Figures 11a and 12a) which correspond to the proposed recruitment time frame for largemouth bass and bluegill in Lake Tahoe (between early July and late August). In later months, mainly larger individuals were captured. For May and June, it is often difficult to discern to what degree size class structure is altered by fish movements from areas with varied thermal regimes versus suspected varying growth rates in Tahoe Keys. In 2007, for both species, the smaller size classes were most prevalent in August with larger individuals captured in June, October and December (Figure 11b and 12b). In 2008, no clear length-based cohorts were observed over time for either species, and smaller size classes were most prevalent in September, but larger individuals were also collected in September and all other sampled months (Figure 11c and 12c).

We also compared our catch data with historical catch records from 1999 and 2003 to examine changes in population dynamics between native and warm-water non-native fishes. Between July and August, the largemouth bass catch in 1999 at Tahoe Keys East (n=61) was dominated by large fish with well defined cohorts according to length-frequency histograms. In 2003 (n=74), 2006 (n=84) and 2007 (n=57) catches were dominated by smaller and younger fish with little definition of length-based cohorts (Figure 13). In 2008, only nine individuals were caught in July and their sizes ranged from small to medium (Figure 13). Bluegill were not caught during electrofishing in 1999, but were caught in 2003 in Tahoe Keys. The absence of bluegill in the 1999 electrofishing sample in Tahoe Keys (Figure 14), both suggest that bluegill became established around 2001. Two modes exist in August 2003 suggesting that only 2 year old bluegill were found at this time. In August 2006 and 2007, and July 2008 the size class structure appeared to be shifting slowly and 3 distinct modes existed in all three years (Figure 14).

A species list is provided for all species caught electrofishing (Table 10). When examining all captured warm-water non-native fishes, before consistent electrofishing occurred in Tahoe Keys and Taylor Creek during the growing season in 2006, the total number of non-native fish captured steadily rose from 1999 until 2006, despite no increase in catch effort (e.g. Tahoe Keys East: Figure 15). In 2007, there was a general decrease in catch of non-native fishes (Figure 15). Total non-native fish captured in May, June, and August 2007 ranged from only 20 %, 35 %, and 38 % of the 2006 capture rate in Tahoe Keys East respectively. In 2008, May capture rate increased slightly to 47% of 2006 capture rate but significant declines in catch in

July and September were observed compared to 2006 and 2007 (Figure 16). In Tahoe Keys West, capture rates in 2007 were 20.3 %, 34.5 %, and 93 % of 2006 capture rates in May, June, and August, respectively (Figure 16). We did not sample Tahoe Keys West in May 2008, but in July and Sept 2008, our combined catch was less than previous years during the same time period (Figure 16). In addition, change in species composition was also observed in 2008, with more brown bullhead catfish caught than in previous years. Much lower capture rates in Tahoe Keys East in 2007 and 2008 suggest that electrofishing during growing season of warm-water non-native fishes could effectively reduce their populations. Decline in catch in Tahoe Keys West in 2007 and 2008 was less than in Tahoe Keys East. This location is situated in the homeowner portion of Tahoe Keys. Better recruitment upon removal at Tahoe Keys West was likely due to greater habitat area and interconnectedness of suitable habitat compared to Tahoe Keys East (Figure 2). For native species, on the other hand, captures declined by 87 % between July and August from 1999 to 2003, thereafter declines continued to 2007 when only 10 native fish were captured in Tahoe Keys East. A slight increase in catch of native species was observed in 2008 (Figure 16), mainly due to an increase in the number of Tahoe Sucker (*Catostomus tahoensis)* caught.

Allometric condition factors (K) were calculated for largemouth bass and bluegill (Figure 17 and 18). Condition factor values (K values) for female largemouth bass exceeded male values at all sites and months except for October in Tahoe Keys East. In contrast, average female K of bluegill was lower than male K in all sites and months except for June in Tahoe Keys West.

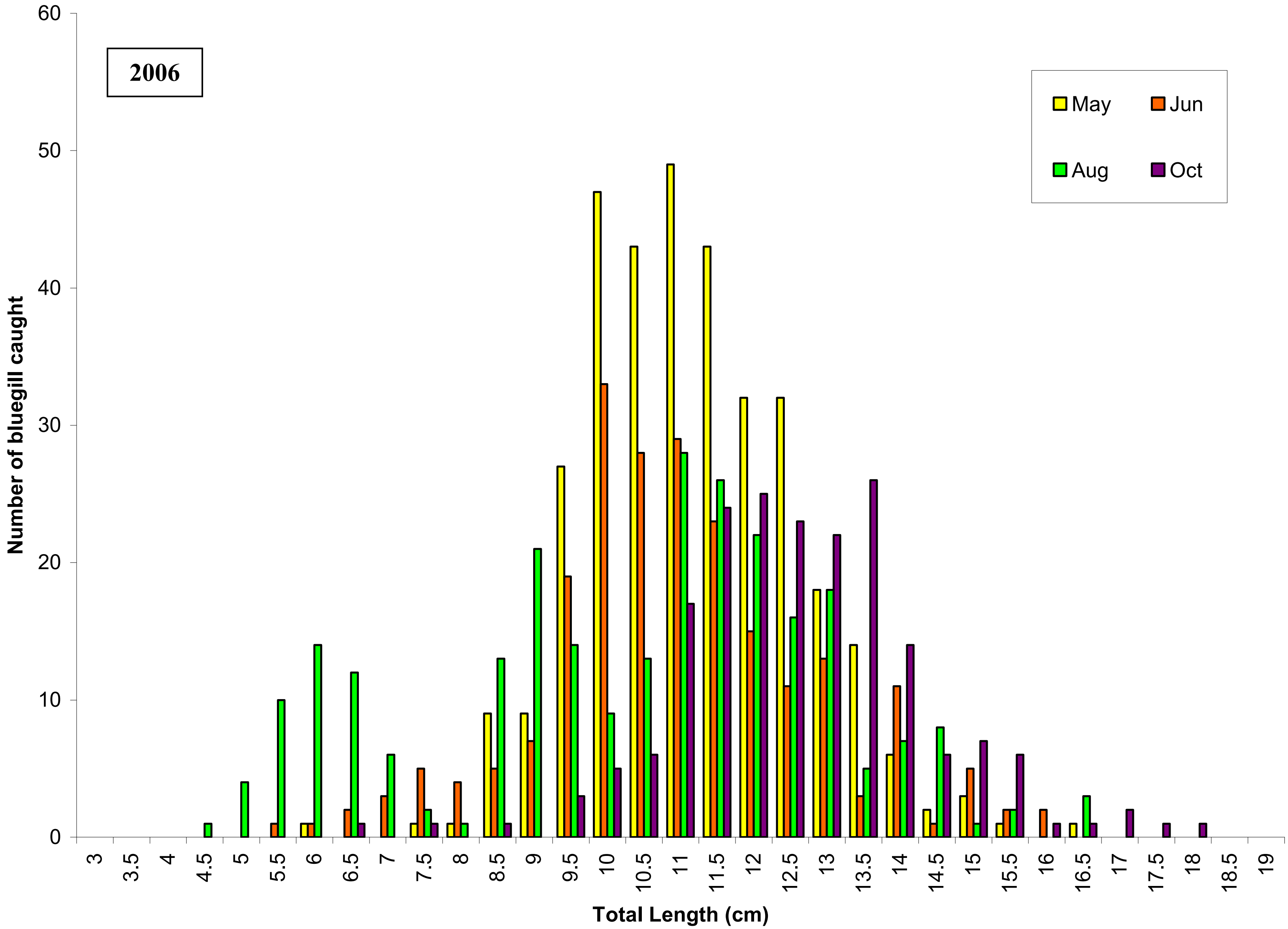


Figure 11a. Bluegill length-frequency distributions for fish captured electrofishing in Tahoe Keys East & West in May, Jun, Aug, and Oct 2006.

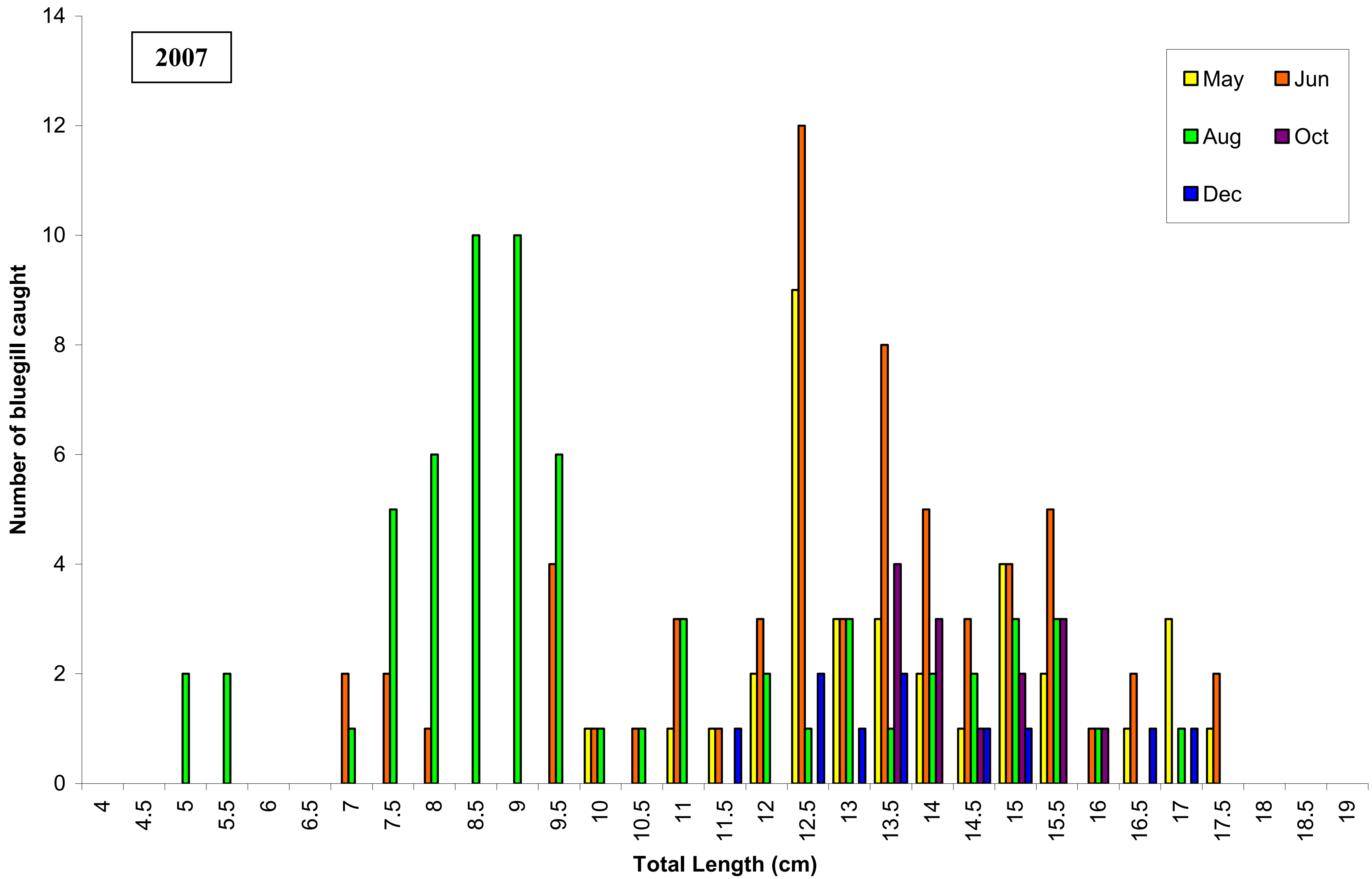


Figure 11b. Bluegill length-frequency distributions for fish captured electrofishing in Tahoe Keys East & West in May, Jun, Aug, Oct, and Dec 2007.

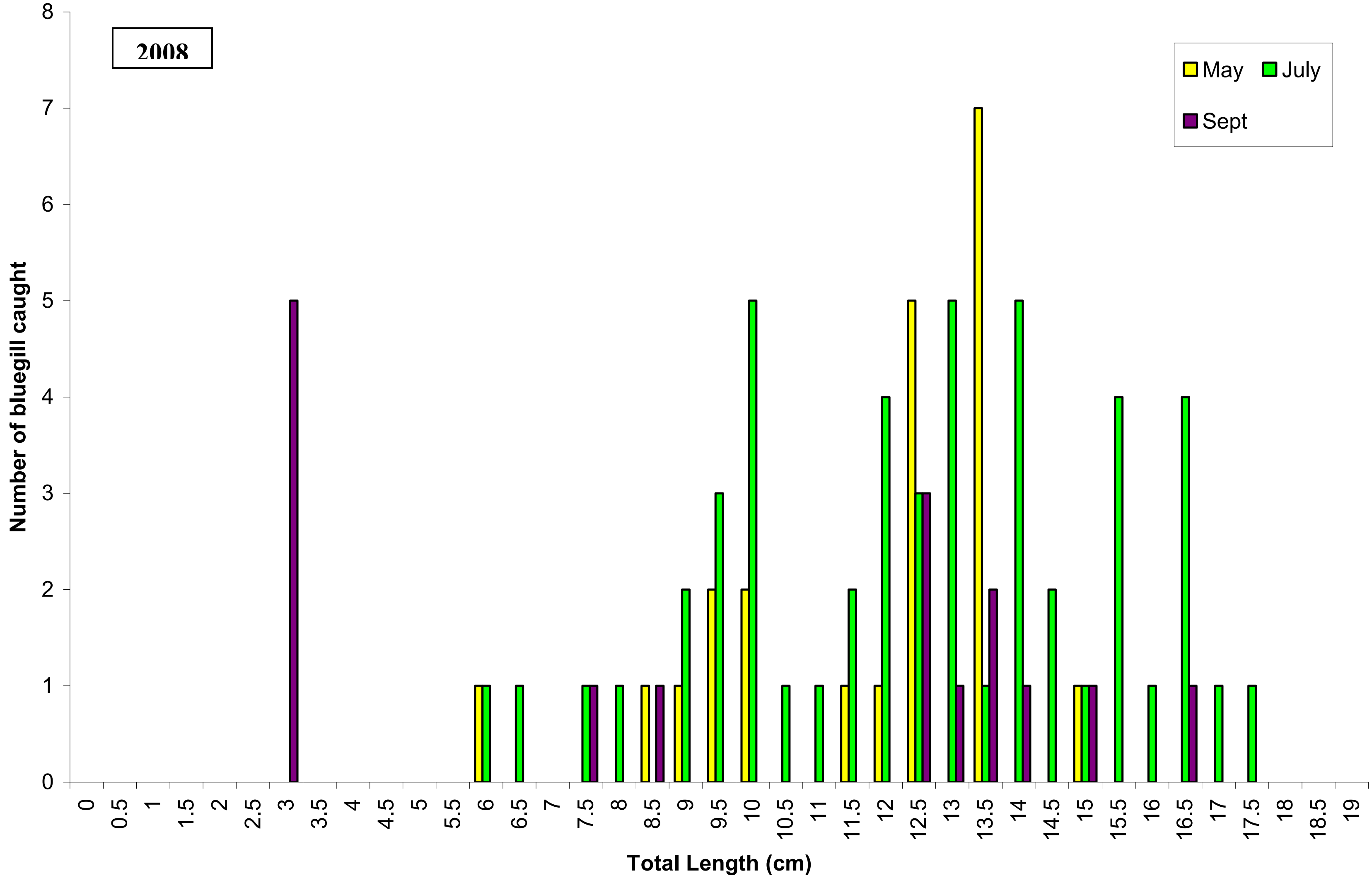


Figure 11c. Bluegill length-frequency distributions for fish captured electrofishing in Tahoe Keys East & West in May, July, and Sept 2008.

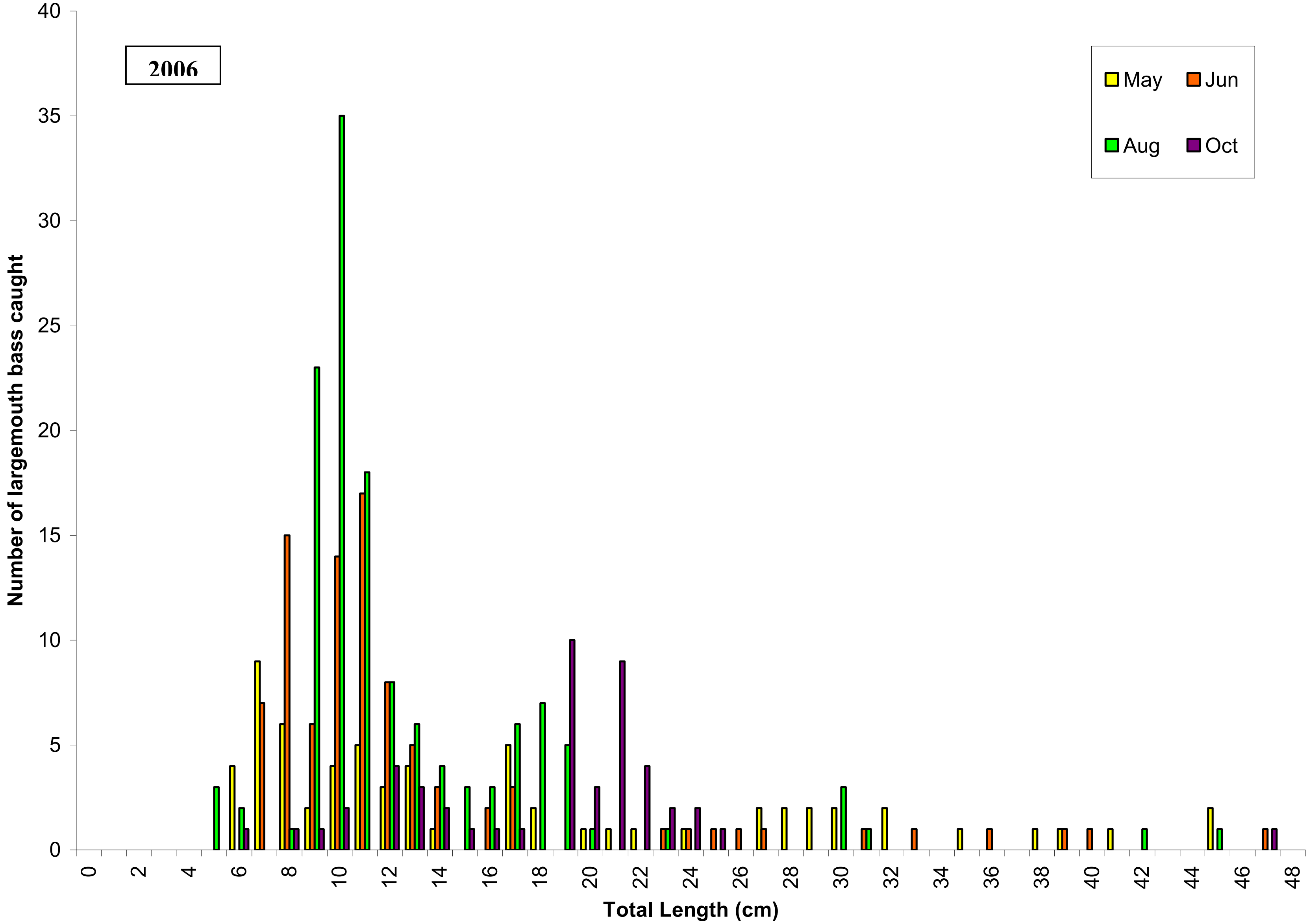


Figure 12a. Largemouth bass length-frequency distributions captured by electrofishing in Tahoe Keys East & West in May, Jun, Aug, and Oct 2006.

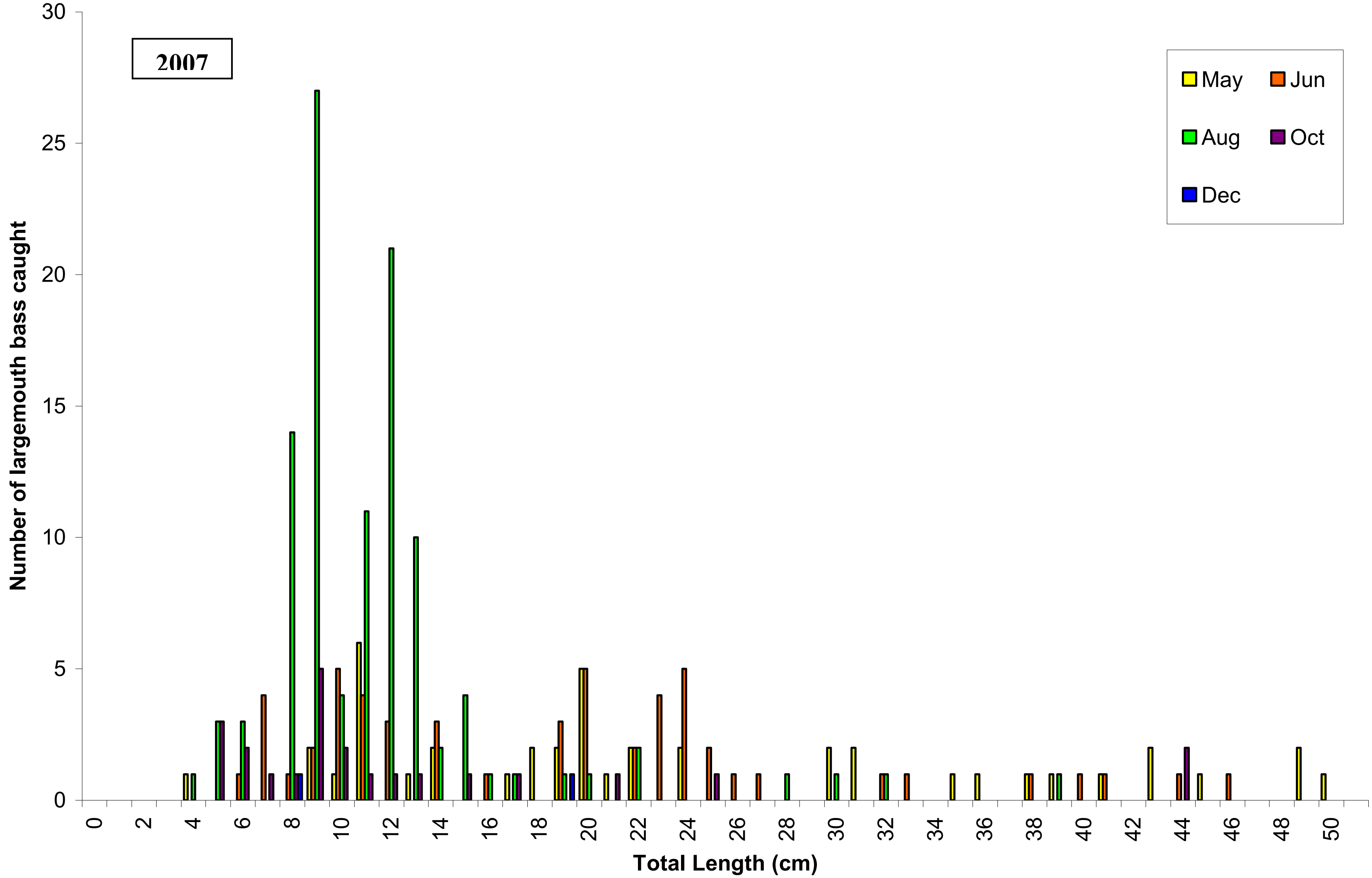


Figure 12b. Largemouth bass length-frequency distributions captured by electrofishing in Tahoe Keys East & West in May, Jun, Aug, Oct, and Dec 2007.

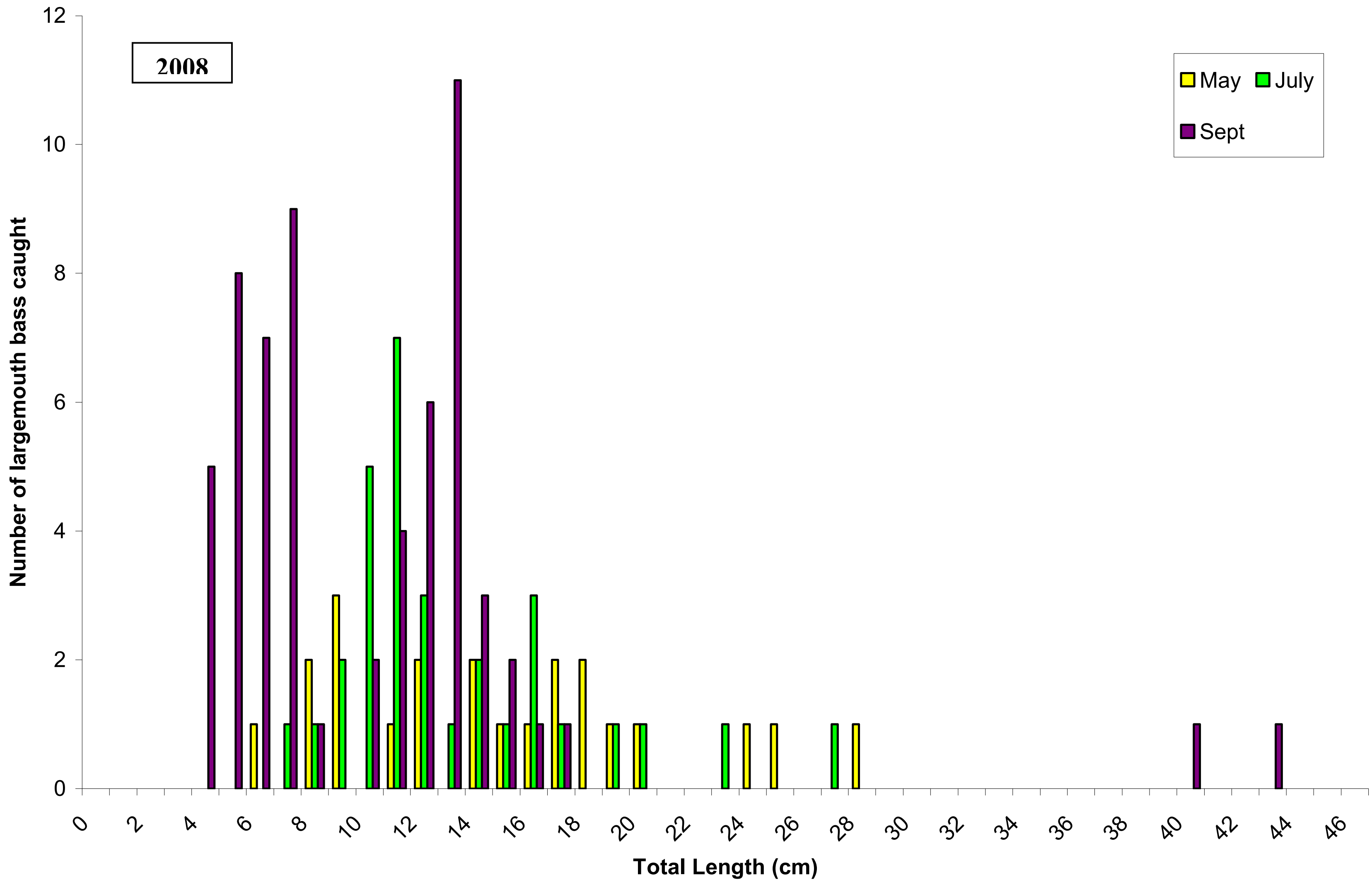


Figure 12c. Largemouth bass length-frequency distributions captured by electrofishing in Tahoe Keys East & West in May, July, and Sept 2008.

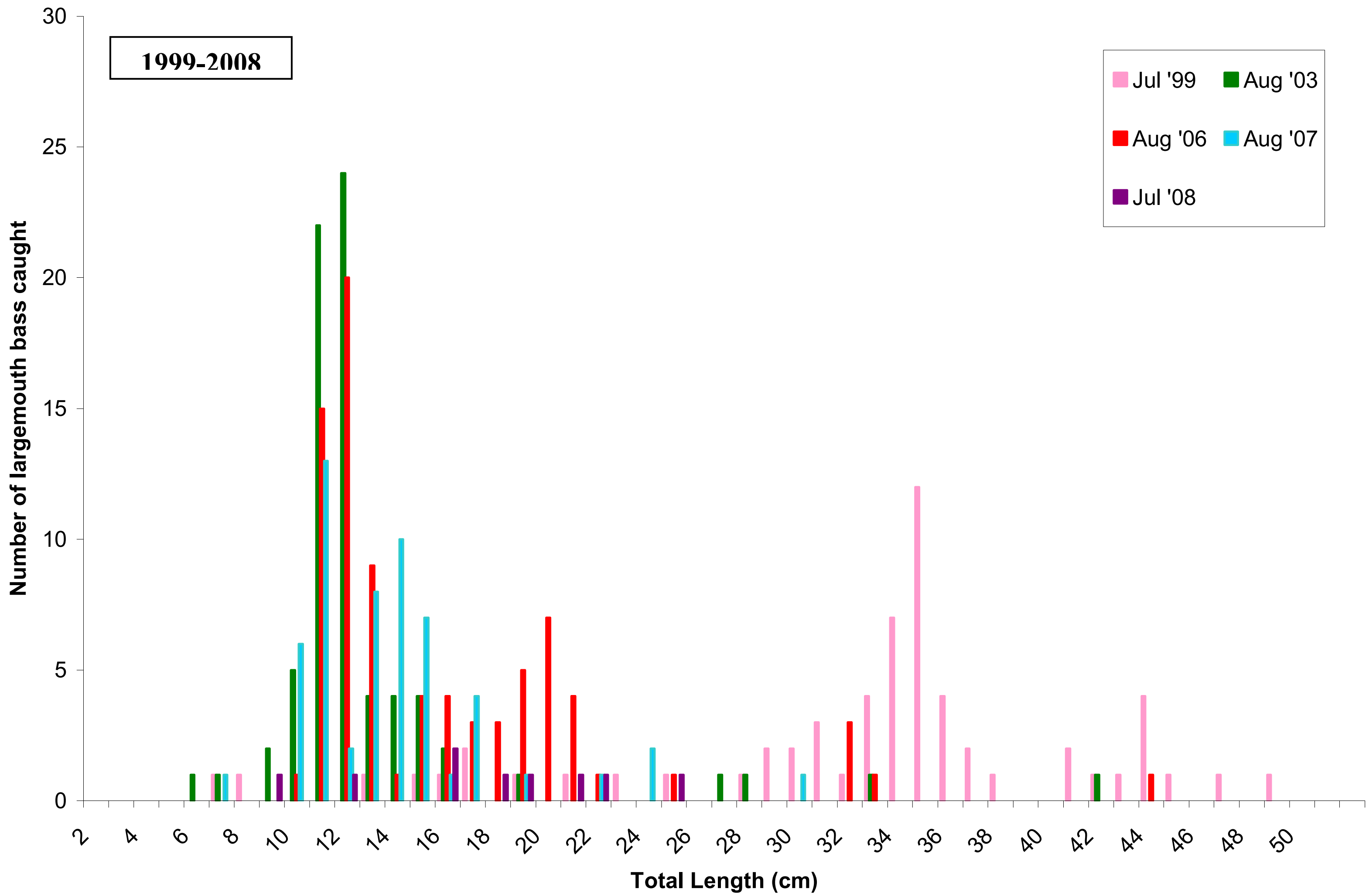


Figure 13. Comparison of largemouth bass length-frequency distributions from Tahoe Keys East in July 1999 and August 2003 to length-frequency distributions from the same location in the current 2006-2008 study. Based on scale ages taken in 2006, a fish of 30 cm total length is 5 to 6 years old.

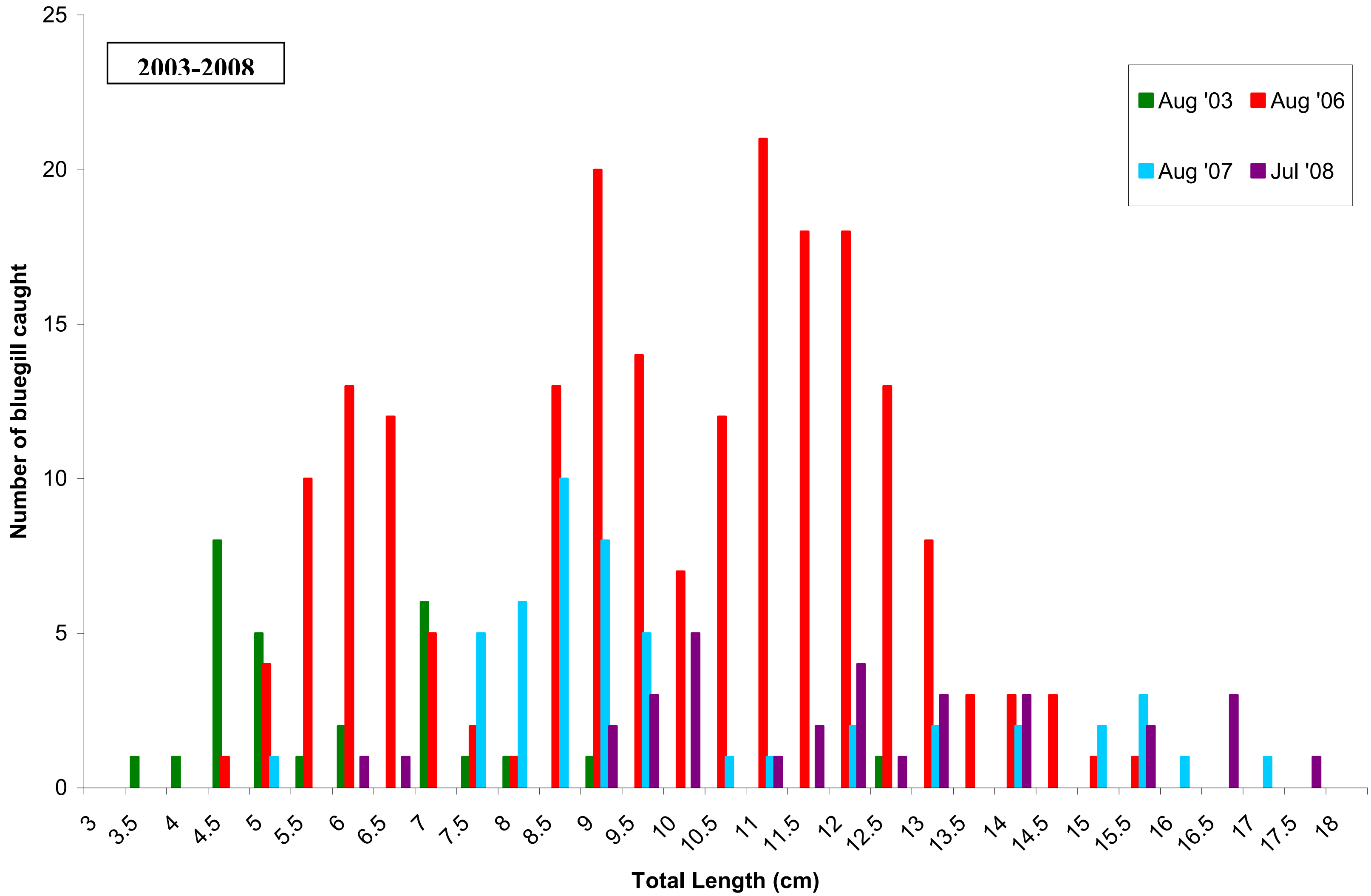


Figure 14. Comparison of bluegill length-frequency distributions from Tahoe Keys East in August 2003 to length-frequency distributions from the same location in the current 2006-2008 study.. Two modes existed in Aug 2003 suggesting that only 2-year-old bluegill were found at this time. In Aug 2006 and 2007, and July 2008 the size class structure appears to be shifting slowly and 3 distinct modes exist in all three year.

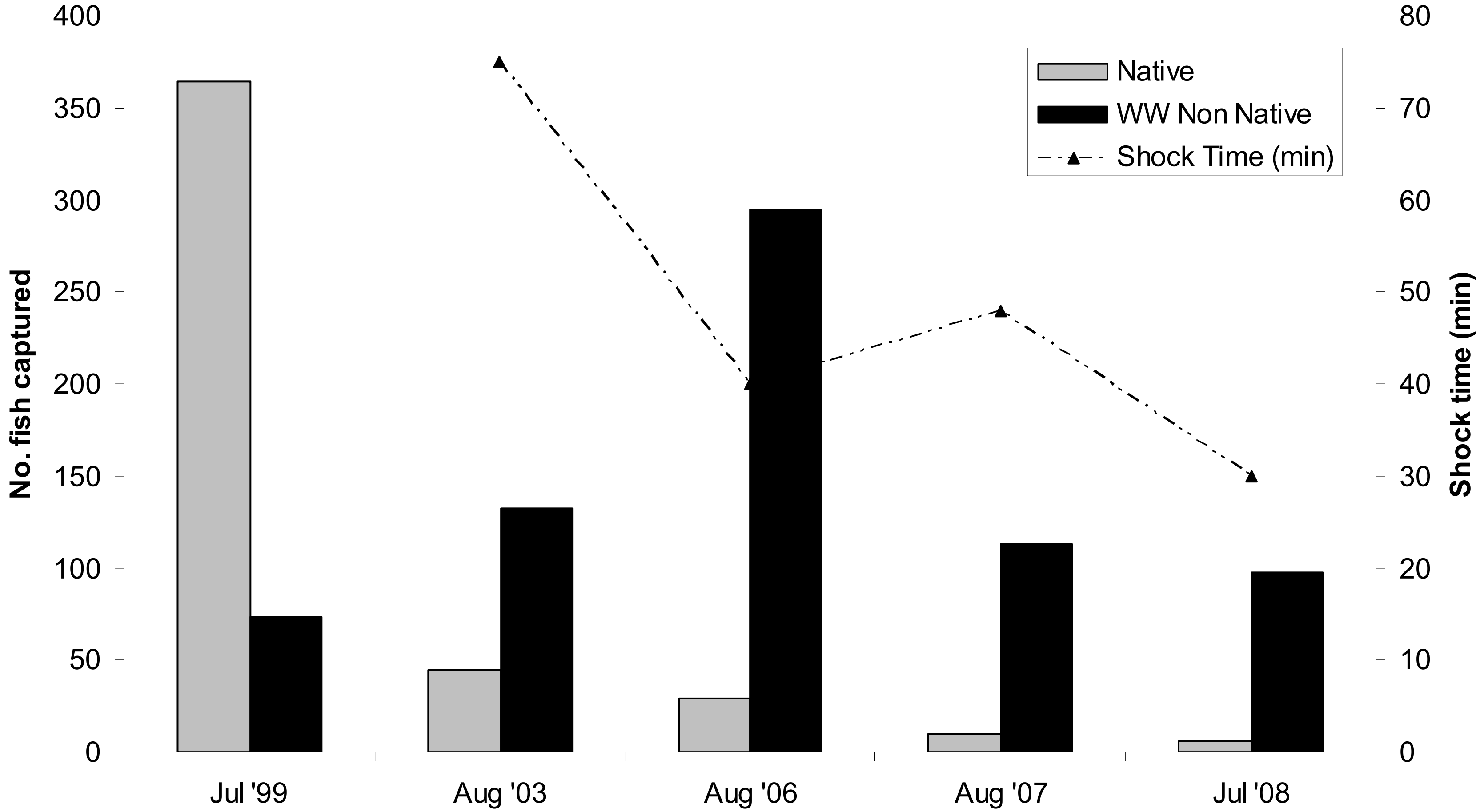


Figure 15. Catch numbers of native fish species and warm-water non-native species during electroshock sampling at Tahoe Keys East in 1999, 2003, and 2006-2008. Sampling dates with the closest proximity among years were chosen for comparison.

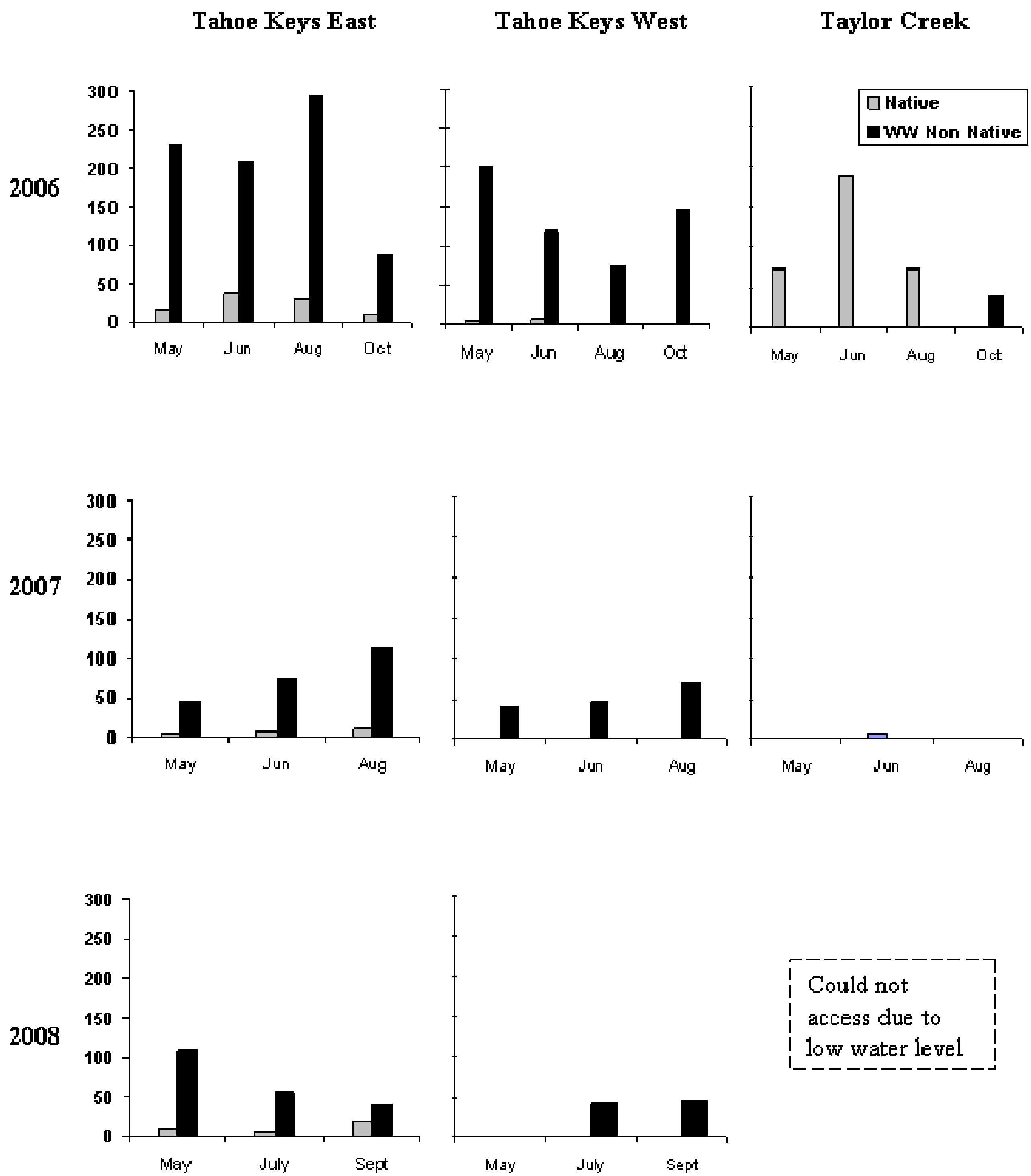


Figure 16. Electroshock results conducted between 2006-2008 from Tahoe Keys East, Tahoe Keys West, and one location at Taylor Creek. Water was too low for boat entry at Taylor Creek during May and Aug 2007 and during the entire sampling season in 2008.

Table 10. Species list of fishes captured in Tahoe Keys East and West during electroshocking in 2006-2008. Species native to Lake Tahoe are indicated by *. All other species are non-native.

| Tahoe Keys Species List 2006-08 | |
|---|---|
| **Common Name** | **Scientific Name** |
| Largemouth Bass | *Micropterus salmoides* |
| Bluegill | *Lepomis macrochirus* |
| Brown Bullhead Catfish | *Ameiurus nebulosus* |
| Black Crappie | *Pomoxis nigromaculatus* |
| Goldfish | *Carassius auratus* |
| Brown trout | *Salmo trutta* |
| Rainbow trout | *Oncorhynchus mykiss* |
| *Tahoe Sucker | *Catostomus tahoensis* |
| *Tui chub | *Gila bicolor* |
| *Lahontan redside shiner | *Richardsonius egregious* |
| *Lahontan speckled dace | *Rhinichthys osculus robustus* |
| *Mountain whitefish | *Prospiu, williamsoni* |

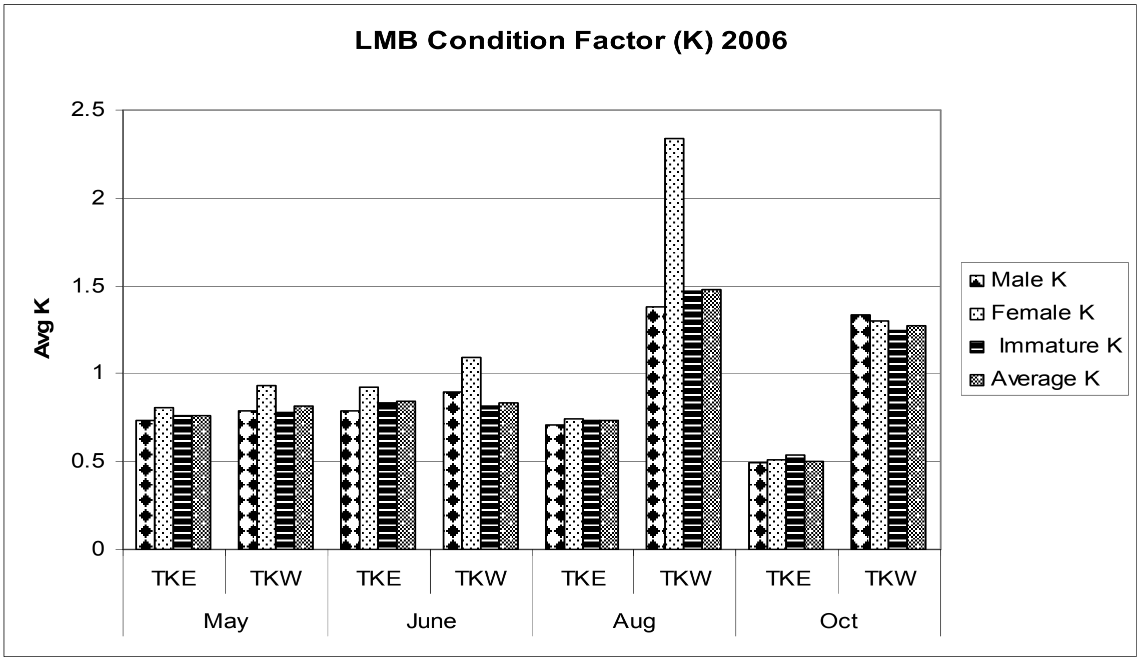


Figure 17. Largemouth bass condition factor (K) for May through Oct 2006. $K=100*L/W^b$; where b is the slope resultant from logarithmic length-weight regression. K is shown for male, female, immature fish and the average of all fish at Tahoe Keys East (TKE) and Tahoe Keys West (TKW).

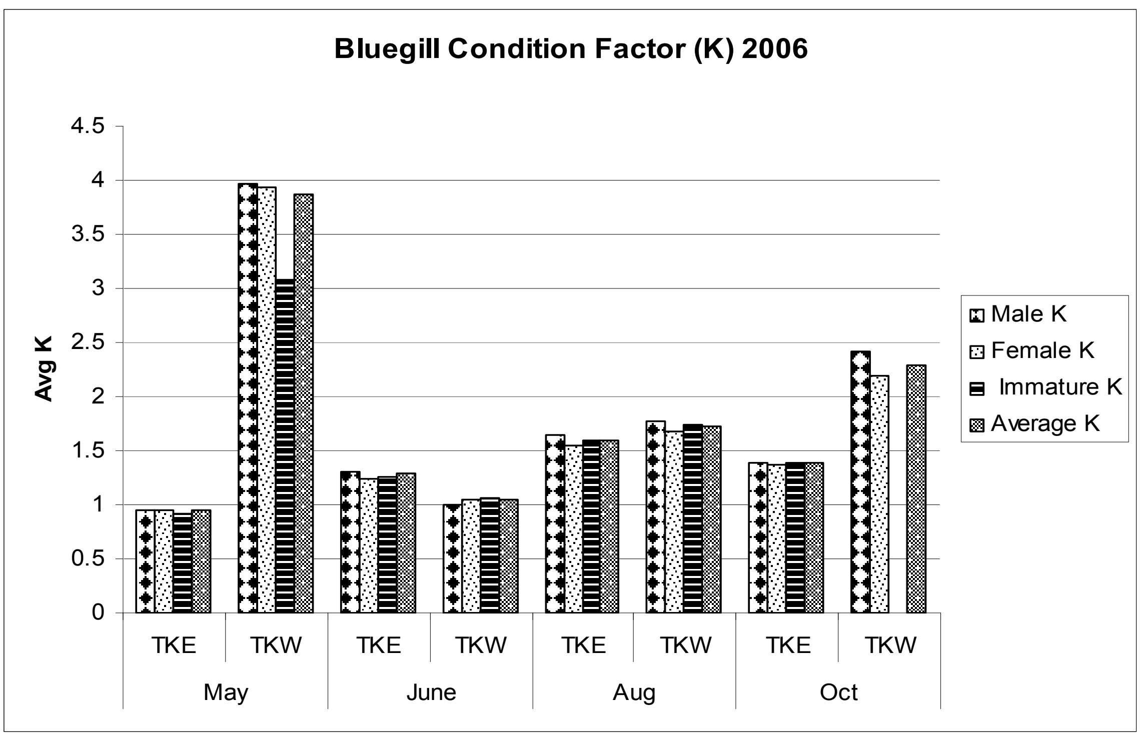


Figure 18. Bluegill condition factor (K) for May through Oct 2006. $K=100*L/W^b$; where b is the slope resultant from logarithmic length-weight regression. K is shown for male, female, immature fish and the average of all fish at Tahoe Keys East (TKE) and Tahoe Keys West (TKW).

*Ageing*

Length-frequency graphs for May and June 2006 for both bluegill (Figure 11a) and largemouth bass (Figure 12a) lack a multimodal distribution. In August and October, three distinct modes occur for bluegill. Consequently, the maximum age from bluegill scales in May, June, and October 2006 was 3++ which equates to a fish on the eve of its $4^{th}$ year. Undefined modes could be indicative of movement of fish to and from sampled sites and multiple spawns in a season which would result in fishes of the same age but varying sizes.

The $R^2$ value from age-length linear regression analysis of bluegill and largemouth bass at each location on sampling dates is presented in Table 11. No significant age-length relationships were derived from bluegill scale ageing, however for largemouth bass, age described most of the variation in length.

The oldest largemouth bass was seven years in 2006 and nine years in 2007. Scale radius, the distance between the focus and anterior margin of the scale, were positively related to total length (n=64, slope=0.899, $R^2$=0.98; Figure 19). Age-length relationships derived from these scales were established for all months. The strength of these relationships decline from June to October 2006 (Figure 20). Scale ages from June 2007 were significantly related to total length (Figure 21).

Table 11. $R^2$ values of linear regression analysis from age-length relationships. Age was determined from scales and standard length was used. '---' indicates that data have not been analyzed for this period.

| | Bluegill | | Largemouth Bass | |
|---|---|---|---|---|
| Month-Year | TKE | TKW | TKE | TKW |
| May-06 | --- | 0.26 | 0.79 | --- |
| Jun-06 | 0.38 | 0.35 | 0.86 | --- |
| Oct-06 | 0.03 | 0.04 | 0.004 | --- |
| May-07 | 0.64 | 0.03 | 0.76 | 0.90 |
| Jun-07 | 0.64 | 0.09 | 0.80 | 0.96 |

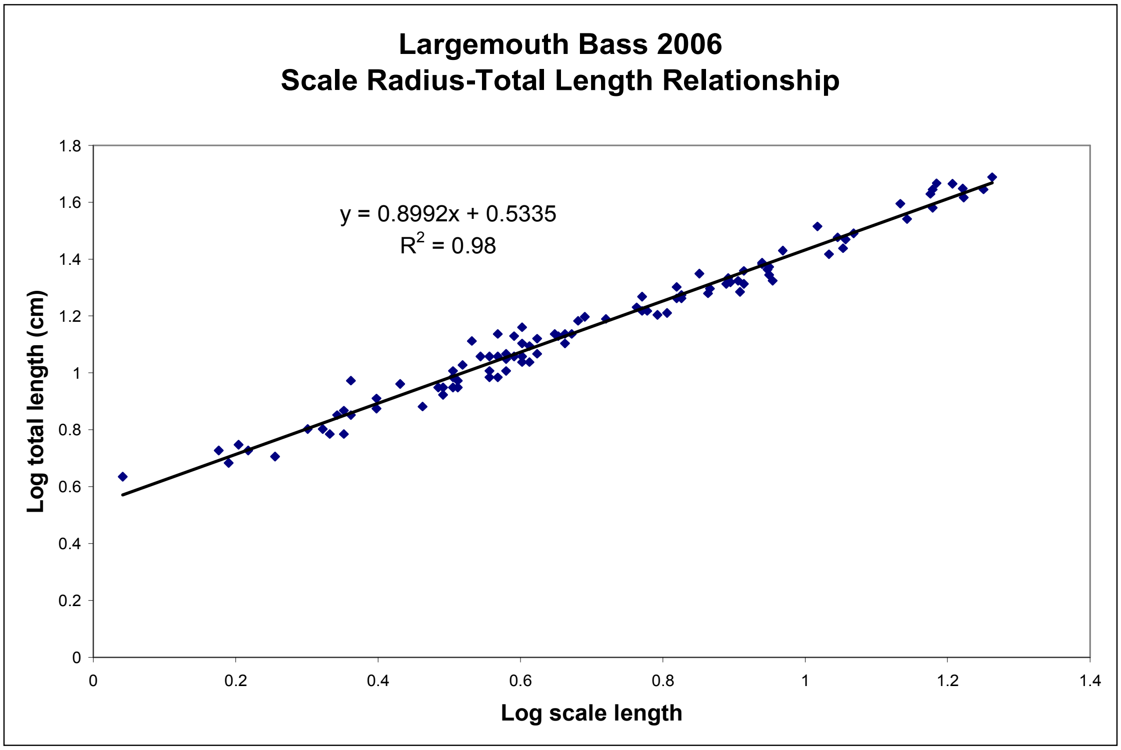


Figure 19. Log regression of scale radius to total length of largemouth bass scales collected in May, Jun, Aug, and Oct of 2006 in Tahoe Keys East and Tahoe Keys West.

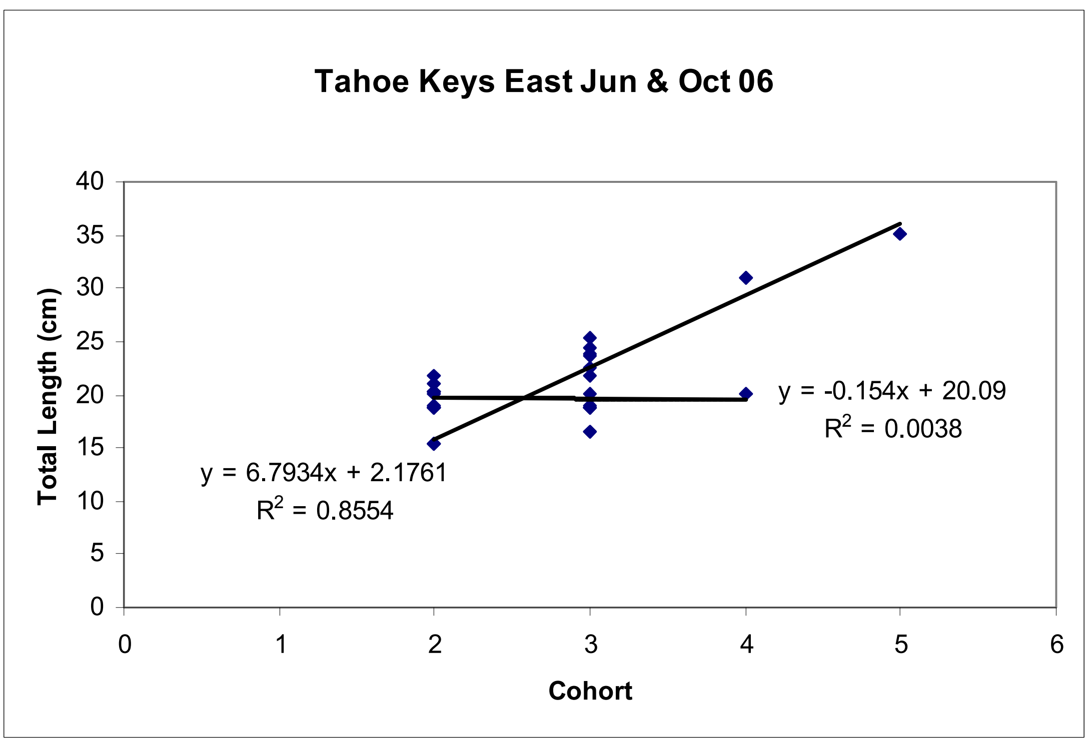


Figure 20. Comparison of cohort age-length relationships in different months from largemouth bass caught in Tahoe Keys East during Jun (n=9) and Oct 2006 (n=22). $R^2$ value drops significantly when marina begins to cool in Oct (Oct $R^2$=0.0038)

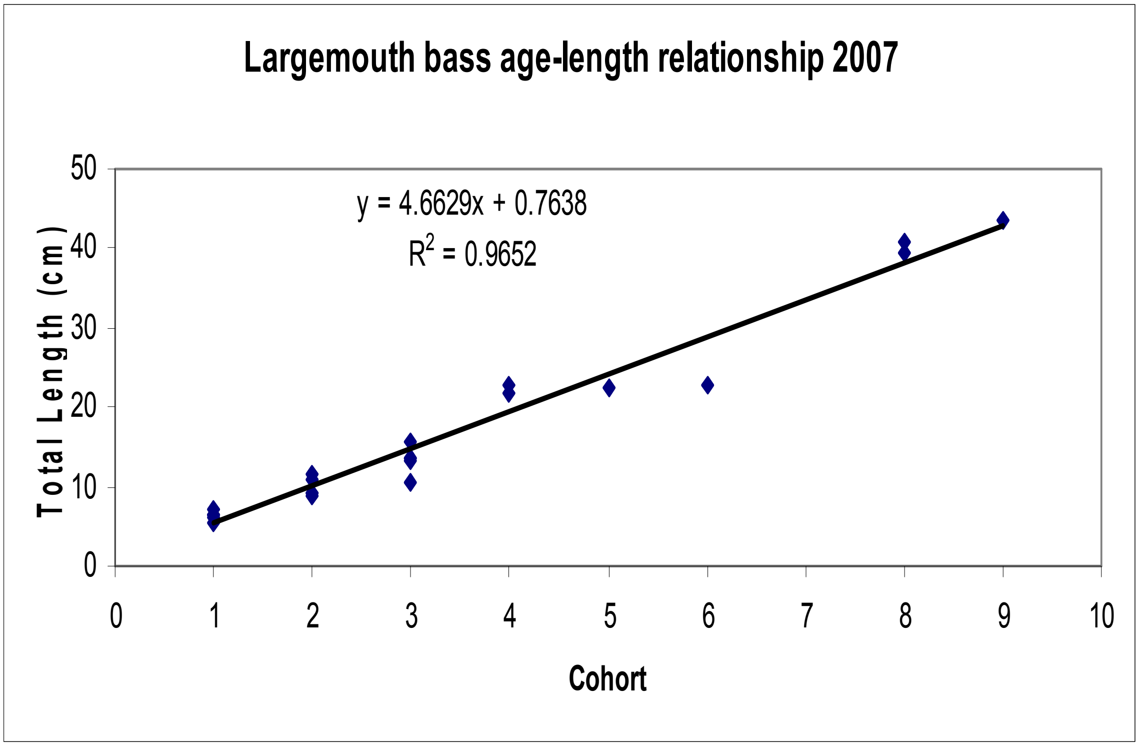


Figure 21. Age-length linear regression of largemouth bass from Tahoe Keys West Jun 2007.

*Diet*

*Bluegill.* To ease interpretation, diet items were grouped into the following categories: zooplankton, unidentified fish, plant material, unidentified invertebrates, Diptera, Ephemeroptera, Mollusca (primarily gastropods with some bi-valves), and terrestrial invertebrates. The proportion by weight of these diet items for all bluegill size classes are shown for May, June, August, and October 2006 (Table 12). Mollusca, plant material, and invertebrates were the three major components of bluegill diets at all sizes in 2006. Gastropods and plant material comprise a majority of the diet in October and May. Aquatic invertebrates, particularly Ephemeroptera dominate June and August diet. Diet breadth was greatest for 10.0-16.0 cm sized fish and lowest for the small and large size classes outside of this range.

Bluegill diet shifts temporally more than ontogenetically. Plant material is the highest proportion of diet for 14.1-16.0 cm total length bluegill until October 2006 when plant proportion decreased for all size classes but 8.1-10.0 cm. All size classes exploited zooplankton, plant, Diptera, Ephemeroptera, and Mollusca. Diet breadth of bluegill and their plasticity in novel environments indicate that bluegill invasion should not be limited by food availability, although growth may differ according to food type.

Percent frequency occurrence indicates zooplankton occurred in 34.2 % of all samples but consisted of only 6.8 % of diet proportion by weight (Table 13). Mollusca were the most frequent item in bluegill diet (48.5± 34.5 %) and contributed the highest proportion to bluegill diet of all sizes in all months (0.31±0.29). Aquatic invertebrates and plant material occur frequently in June and August. Higher predation rates on zooplankton likely reduce water clarity, and increase competition for food where non-native fishes occur. Based on historical native fish diet studies and the results of non-native fish diets, bluegill diets overlap with native fish diets (Kamerath et al. 2008).

Table 12. Diet-item proportion by weight of total diet for bluegill size classes in May, Jun, Aug, and Oct 2006. Empty stomachs occurred where zeros exist under each diet item.

| Month | Size Class (cm) | Zooplankton | Unid Fish | Plant | Diptera | Aquatic Invt. | Ephemeroptera | Mollusca | Amphipod | Terrestrial Invt. |
|---|---|---|---|---|---|---|---|---|---|---|
| May | 4.1-6.0 | 0.000 | 0.000 | 0.231 | 0.015 | 0.000 | 0.000 | 0.723 | 0.031 | 0.000 |
| | 6.1-8.0 | 0.274 | 0.000 | 0.153 | 0.463 | 0.111 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 8.1-10.0 | 0.061 | 0.000 | 0.180 | 0.045 | 0.083 | 0.022 | 0.607 | 0.002 | 0.001 |
| | 10.1-12.0 | 0.088 | 0.000 | 0.173 | 0.113 | 0.054 | 0.004 | 0.567 | 0.000 | 0.000 |
| | 12.1-14.0 | 0.038 | 0.000 | 0.243 | 0.208 | 0.127 | 0.020 | 0.346 | 0.005 | 0.013 |
| | 14.1-16.0 | 0.008 | 0.000 | 0.671 | 0.052 | 0.009 | 0.006 | 0.254 | 0.000 | 0.000 |
| | 16.1+ | 0.108 | 0.000 | 0.124 | 0.317 | 0.425 | 0.000 | 0.000 | 0.000 | 0.027 |
| Jun | 4.1-6.0 | 0.000 | 0.000 | 0.000 | 0.029 | 0.000 | 0.946 | 0.026 | 0.000 | 0.000 |
| | 6.1-8.0 | 0.007 | 0.000 | 0.003 | 0.092 | 0.058 | 0.510 | 0.301 | 0.000 | 0.030 |
| | 8.1-10.0 | 0.041 | 0.000 | 0.041 | 0.206 | 0.028 | 0.441 | 0.242 | 0.001 | 0.000 |
| | 10.1-12.0 | 0.037 | 0.000 | 0.062 | 0.148 | 0.024 | 0.474 | 0.240 | 0.002 | 0.014 |
| | 12.1-14.0 | 0.020 | 0.000 | 0.187 | 0.105 | 0.152 | 0.211 | 0.315 | 0.000 | 0.010 |
| | 14.1-16.0 | 0.009 | 0.000 | 0.877 | 0.023 | 0.030 | 0.057 | 0.002 | 0.000 | 0.002 |
| | 16.1+ | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Aug | 4.1-6.0 | 0.128 | 0.000 | 0.000 | 0.670 | 0.006 | 0.000 | 0.099 | 0.096 | 0.000 |
| | 6.1-8.0 | 0.441 | 0.159 | 0.000 | 0.366 | 0.028 | 0.000 | 0.000 | 0.007 | 0.000 |
| | 8.1-10.0 | 0.047 | 0.002 | 0.262 | 0.230 | 0.020 | 0.045 | 0.347 | 0.005 | 0.042 |
| | 10.1-12.0 | 0.001 | 0.000 | 0.153 | 0.129 | 0.014 | 0.026 | 0.673 | 0.000 | 0.004 |
| | 12.1-14.0 | 0.000 | 0.000 | 0.444 | 0.232 | 0.079 | 0.014 | 0.197 | 0.016 | 0.018 |
| | 14.1-16.0 | 0.000 | 0.000 | 0.761 | 0.149 | 0.044 | 0.000 | 0.040 | 0.000 | 0.007 |
| | 16.1+ | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Oct | 4.1-6.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 6.1-8.0 | 0.500 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.333 | 0.167 | 0.000 |
| | 8.1-10.0 | 0.005 | 0.000 | 0.177 | 0.010 | 0.190 | 0.000 | 0.249 | 0.369 | 0.000 |
| | 10.1-12.0 | 0.024 | 0.000 | 0.003 | 0.191 | 0.005 | 0.000 | 0.704 | 0.073 | 0.000 |
| | 12.1-14.0 | 0.023 | 0.000 | 0.006 | 0.107 | 0.013 | 0.001 | 0.829 | 0.021 | 0.000 |
| | 14.1-16.0 | 0.044 | 0.000 | 0.003 | 0.102 | 0.006 | 0.001 | 0.823 | 0.020 | 0.001 |
| | 16.1+ | 0.014 | 0.000 | 0.023 | 0.102 | 0.026 | 0.001 | 0.783 | 0.045 | 0.006 |

Table 13. Percent frequency occurrence of diet item in bluegill stomachs of different size classes in May, Jun, Aug, and Oct 2006.

| Month | Size Class (cm) | Zooplankton | Unid. Fish | Plant | Diptera | Aquatic Invert. | Ephemeroptera | Mollusca | Amphipod | Terrestrial Invert. |
|---|---|---|---|---|---|---|---|---|---|---|
| May | 4.1-6.0 | 0 | 0 | 100 | 100 | 0 | 0 | 100 | 100 | 0 |
| | 6.1-8.0 | 100 | 0 | 33 | 100 | 0 | 33 | 0 | 0 | 0 |
| | 8.1-10.0 | 42 | 0 | 56 | 64 | 28 | 44 | 47 | 6 | 6 |
| | 10.1-12.0 | 43 | 0 | 50 | 67 | 23 | 10 | 43 | 7 | 3 |
| | 12.1-14.0 | 43 | 0 | 57 | 91 | 20 | 49 | 54 | 14 | 26 |
| | 14.1-16.0 | 25 | 0 | 75 | 75 | 25 | 0 | 50 | 0 | 0 |
| | 16.1+ | 100 | 0 | 100 | 100 | 0 | 0 | 0 | 0 | 100 |
| June | 4.1-6.0 | 0 | 0 | 0 | 100 | 100 | 0 | 100 | 0 | 0 |
| | 6.1-8.0 | 67 | 0 | 11 | 67 | 89 | 44 | 78 | 0 | 22 |
| | 8.1-10.0 | 40 | 0 | 28 | 92 | 100 | 24 | 52 | 16 | 0 |
| | 10.1-12.0 | 33 | 0 | 46 | 96 | 83 | 21 | 50 | 8 | 8 |
| | 12.1-14.0 | 20 | 0 | 37 | 93 | 67 | 37 | 47 | 3 | 23 |
| | 14.1-16.0 | 22 | 0 | 67 | 89 | 100 | 44 | 11 | 0 | 33 |
| | 16.1+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aug | 4.1-6.0 | 27 | 0 | 0 | 64 | 0 | 9 | 18 | 36 | 0 |
| | 6.1-8.0 | 50 | 17 | 0 | 67 | 0 | 0 | 0 | 17 | 0 |
| | 8.1-10.0 | 14 | 7 | 43 | 64 | 29 | 21 | 50 | 14 | 14 |
| | 10.1-12.0 | 14 | 0 | 36 | 71 | 21 | 36 | 71 | 7 | 7 |
| | 12.1-14.0 | 4 | 0 | 43 | 87 | 9 | 13 | 39 | 30 | 17 |
| | 14.1-16.0 | 0 | 0 | 80 | 100 | 0 | 20 | 60 | 0 | 20 |
| | 16.1+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Oct | 4.1-6.0 | 100 | 0 | 0 | 0 | 0 | 0 | 100 | 100 | 0 |
| | 6.1-8.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 8.1-10.0 | 22 | 0 | 22 | 11 | 0 | 67 | 44 | 67 | 0 |
| | 10.1-12.0 | 33 | 0 | 8 | 54 | 0 | 42 | 67 | 42 | 4 |
| | 12.1-14.0 | 54 | 0 | 19 | 72 | 9 | 41 | 89 | 52 | 4 |
| | 14.1-16.0 | 38 | 0 | 13 | 63 | 6 | 25 | 88 | 38 | 13 |
| | 16.1+ | 67 | 0 | 67 | 100 | 50 | 83 | 100 | 83 | 17 |

*Largemouth Bass.* The proportion by weight that each diet item contributed to largemouth bass total diet is reported in Table 14. Percent frequency occurrence is shown for each size class per month for largemouth bass (Table 15). Largemouth bass diet composition shifts ontogenetically and seasonally. Zooplankton comprised an average of 48.6 % of the diet for fish 4.0-8.1 cm in length. Zooplankton were not utilized by fish greater than 16.0 cm in total length. Diet breadth, unlike bluegill, decreased with length and thus age (Figure 22). Largemouth bass first exhibited piscivory at 8.1-12.0 cm total length and fish comprised 12-68 % of the diet from this size through >40.1 cm. Decapoda were only consumed by fish > 8.0 cm total length, and Decapod contribution to the diet increased with fish size until Decapoda contributed 45 % of the diet for fish 20.1-24.0 cm total length. Sample size also decreased with fish length, therefore dietary snapshots are not equally represented for the larger size classes.

Mollusca were found in both the largest and smallest size classes. Invertebrates comprised the majority of all diets in May and June, while plant, fish and Mollusca were found in higher proportion in May and October 2006. Fish and aquatic invertebrates were the most common diet items among size classes, being found in 6 of 8 size classes. Fish were found in the diet only during August and October 2006.

Diet analysis confirmed that bluegill of all sizes exploit myriad diet items, including those consumed by native fishes (Miller 1951). Largemouth bass first became piscivorous at two to four years (8.0-12.0 cm) according to age-length relationships derived from scales collected in 2007. Thus to minimize predation pressure and competition on native fishes, non-native fishes, particularly largemouth bass, should be removed at a minimum of three year intervals. It is suggested that two consecutive years of management should occur first to reduce or eliminate satellite populations outside of Tahoe Keys. Optimally, removal efforts should occur on a two year interval for both largemouth bass and bluegill.

Table 14. Diet item proportion of total diet for largemouth bass size classes in May, Jun, Aug, and Oct 2006. Empty stomachs occur where zeros exist under each diet item. Blank lines indicate no fish of this size class were caught that month. Note that these proportions are different from diet proportions in Table 6 because bass are categorized by length instead of by cohort, for comparison with bluegill.

| Month | Size Class (cm) | Zoop | Unid fish | LMB fish | Redside fish | Plant | Diptera | Aquatic Invert. | Ephemeroptera | Mollusca | Amphipod | Terrestrial Invert | Decapod |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| May | 4.0-8.0 | 0.313 | 0.000 | 0.000 | 0.000 | 0.003 | 0.231 | 0.159 | 0.034 | 0.065 | 0.082 | 0.003 | 0.000 |
| | 8.1-12.0 | 0.155 | 0.005 | 0.000 | 0.000 | 0.005 | 0.258 | 0.009 | 0.089 | 0.000 | 0.014 | 0.005 | 0.000 |
| | 12.1-16.0 | 0.160 | 0.280 | 0.000 | 0.000 | 0.000 | 0.053 | 0.000 | 0.173 | 0.000 | 0.013 | 0.000 | 0.000 |
| | 16.1-20.0 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 20.1-24.0 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 24.1-30.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 30.1-40.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 40.1++ | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Jun | 4.0-8.0 | 0.023 | 0.000 | 0.000 | 0.000 | 0.000 | 0.078 | 0.157 | 0.687 | 0.000 | 0.012 | 0.015 | 0.000 |
| | 8.1-12.0 | 0.012 | 0.000 | 0.000 | 0.000 | 0.006 | 0.097 | 0.116 | 0.571 | 0.002 | 0.001 | 0.003 | 0.000 |
| | 12.1-16.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.132 | 0.142 | 0.713 | 0.000 | 0.000 | 0.000 | 0.013 |
| | 16.1-20.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 20.1-24.0 | | | | | | | | | | | | |
| | 24.1-30.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 30.1-40.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 40.1++ | | | | | | | | | | | | |
| Aug | 4.0-8.0 | 0.608 | 0.000 | 0.000 | 0.000 | 0.000 | 0.085 | 0.161 | 0.000 | 0.000 | 0.050 | 0.000 | 0.000 |
| | 8.1-12.0 | 0.011 | 0.258 | 0.000 | 0.000 | 0.000 | 0.056 | 0.192 | 0.002 | 0.002 | 0.019 | 0.052 | 0.328 |
| | 12.1-16.0 | 0.000 | 0.168 | 0.000 | 0.000 | 0.000 | 0.016 | 0.192 | 0.001 | 0.000 | 0.004 | 0.025 | 0.363 |
| | 16.1-20.0 | 0.000 | 0.154 | 0.000 | 0.000 | 0.000 | 0.006 | 0.000 | 0.000 | 0.000 | 0.000 | 0.010 | 0.808 |
| | 20.1-24.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 |
| | 24.1-30.0 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 30.1-40.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 40.1++ | 0.000 | 0.999 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 |
| Oct | 4.0-8.0 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 8.1-12.0 | 0.050 | 0.868 | 0.000 | 0.000 | 0.000 | 0.050 | 0.000 | 0.000 | 0.000 | 0.023 | 0.000 | 0.000 |
| | 12.1-16.0 | 0.000 | 0.046 | 0.953 | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 16.1-20.0 | 0.000 | 0.480 | 0.000 | 0.000 | 0.000 | 0.000 | 0.047 | 0.000 | 0.000 | 0.000 | 0.030 | 0.443 |
| | 20.1-24.0 | 0.000 | 0.295 | 0.024 | 0.292 | 0.000 | 0.000 | 0.018 | 0.000 | 0.000 | 0.000 | 0.000 | 0.371 |
| | 24.1-30.0 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 30.1-40.0 | | | | | | | | | | | | |
| | 40.1++ | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

Table 15. Percent frequency occurrence of diet item in largemouth bass stomachs of different size classes in May, Jun, Aug, and Oct 2006. LMB is largemouth bass.

| Month | Size Class (cm) | Zoop | Unid fish | LMB fish | Redside fish | Plant | Diptera | Aquatic Invert | Ephemeroptera | Amphipod | Terrestrial Invert | Decapod |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| May | 4.1-8.0 | 50 | 0 | 0 | 0 | 6 | 67 | 67 | 11 | 0 | 0 | 0 |
| | 8.1-12.0 | 25 | 8 | 0 | 0 | 8 | 42 | 67 | 17 | 0 | 0 | 0 |
| | 12.1-16.0 | 20 | 40 | 0 | 0 | 0 | 20 | 40 | 20 | 0 | 0 | 0 |
| | 16.1-20.0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 20.1-24.0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 24.1-30.0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 0 | 0 | 0 | 0 |
| | 30.1-40.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 40.1+ | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| June | 4.1-8.0 | 29 | 0 | 0 | 0 | 0 | 71 | 62 | 86 | 0 | 6 | 0 |
| | 8.1-12.0 | 15 | 0 | 0 | 0 | 5 | 80 | 51 | 80 | 2 | 8 | 0 |
| | 12.1-16.0 | 0 | 0 | 0 | 0 | 0 | 50 | 17 | 83 | 0 | 0 | 17 |
| | 16.1-20.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 20.1-24.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 24.1-30.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 30.1-40.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 40.1+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aug | 4.1-8.0 | 83 | 0 | 0 | 0 | 0 | 67 | 83 | 0 | 0 | 19 | 0 |
| | 8.1-12.0 | 21 | 9 | 0 | 0 | 2 | 46 | 49 | 5 | 0 | 17 | 7 |
| | 12.1-16.0 | 0 | 13 | 0 | 0 | 0 | 13 | 60 | 7 | 0 | 0 | 20 |
| | 16.1-20.0 | 0 | 11 | 0 | 0 | 0 | 5 | 5 | 0 | 0 | 0 | 21 |
| | 20.1-24.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| | 24.1-30.0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 30.1-40.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 40.1+ | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Oct | 4.1-8.0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 8.1-12.0 | 43 | 14 | 0 | 0 | 0 | 29 | 14 | 0 | 0 | 22 | 0 |
| | 12.1-16.0 | 0 | 14 | 14 | 0 | 0 | 14 | 0 | 0 | 0 | 20 | 0 |
| | 16.1-20.0 | 0 | 45 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 5 | 9 |
| | 20.1-24.0 | 0 | 30 | 10 | 10 | 0 | 0 | 10 | 0 | 0 | 0 | 10 |
| | 24.1-30.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 30.1-40.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 40.1+ | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 |

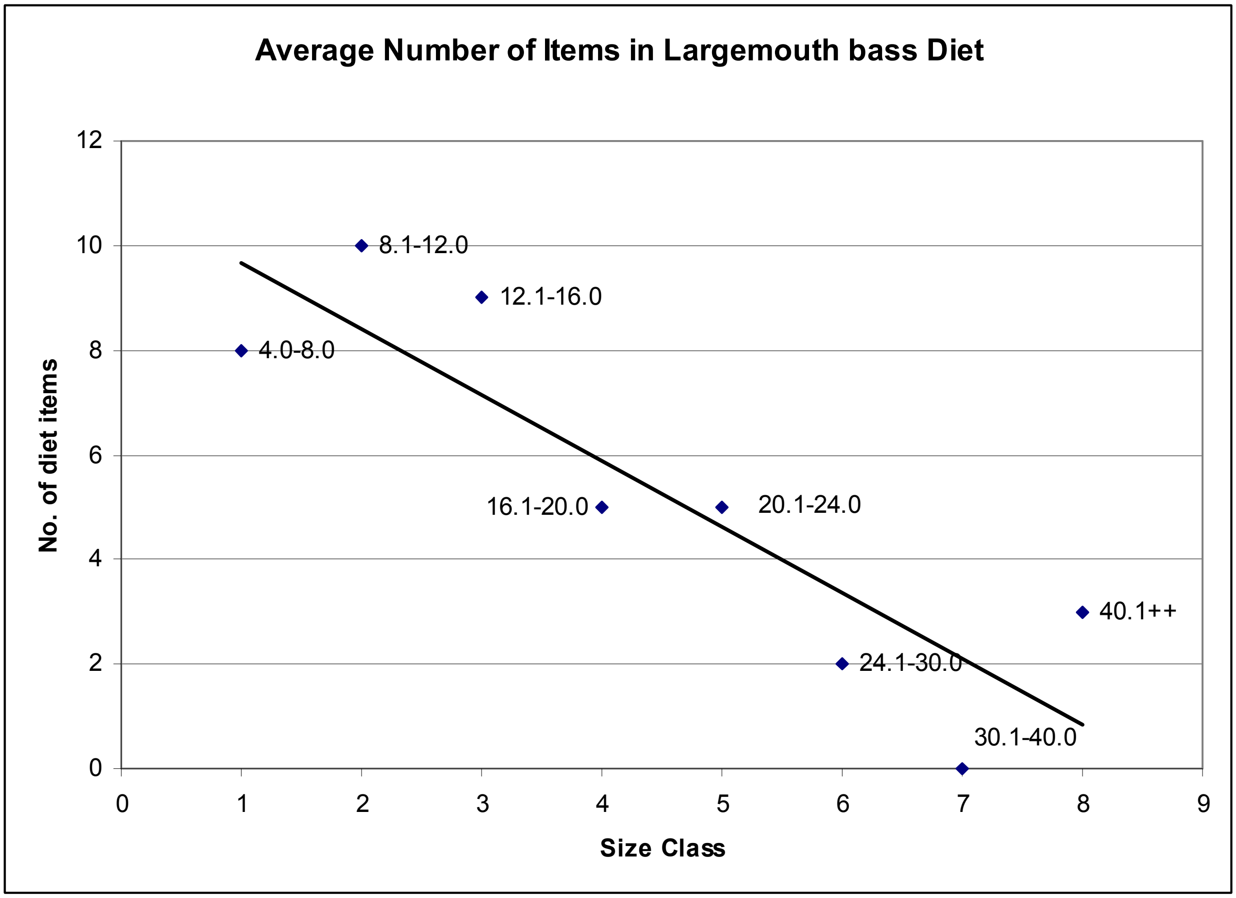


Figure 22. Diet breadth decreases with length (and therefore age) of largemouth bass sampled in the Tahoe Keys during May-Oct 2006. Size class is plotted next to each data point.

*Surface water temperature*

Surface water temperature data collected in 2006-2008 revealed that suitable spawning temperatures for bluegill and largemouth bass existed at all monitored sites including those without non-native fish presence (Tables 11 and 12). We assumed 15.9 ºC as the minimum spawning temperature for largemouth bass (Strawn 1961, Kramer and Smith 1960) and 18 ºC the minimum for bluegill (Moyle 1976). Under these assumptions, all monitored sites reached suitable spawning temperatures in all three sampling years (2006-2008; Tables 11 and 12).

For all sampled sites, minimum spawning temperature for bluegill was met or exceeded between June 20 to July 15, 2006, May 28 to July 23, 2007, and June 9 to August 5, 2008 (Table 16). Snorkel observations from 2006-2007 confirm that at least bluegill were spawning outside of Tahoe Keys and both largemouth bass and bluegill spawned within Tahoe Keys. During 2007 bluegill were observed nest guarding behind the Fresh Ketch restaurant in Tahoe Keys East on 03 July and spawning behind the boat rental shop on Jul 18, 2007. Water temperature at the nest site during spawning was 22.17 ºC. Bluegill were guarding nests on Jul 31 and Aug 15 in Ski-Run and Lakeside Marina, respectively. Eleven young-of-year bluegill were observed at Sierra Boat Works in Carnelian Bay on Aug 1, 2007. In 2008, 6 bluegill were observed nest guarding at the same area on July 17when water temperature was around 23 ºC. To prevent bluegill spawning and additional recruitment, management of existing populations should occur in late June in Tahoe Keys and in middle July outside of Tahoe Keys or before temperatures consistently exceed 18-20 ºC within respective locations.

Minimum spawning temperature for largemouth bass was first met or exceeded between May 13 to June 29 in 2006, May 15 to July 5 in 2007, and May 14 to August 5 in 2008 (Table 16). In 2007, homeowners reported spawning behavior in Tahoe Keys West (Figure 2), an area in the homeowner portion of Tahoe Keys, on or near June 5. A largemouth bass nest was confirmed on June 20 behind Fresh Ketch restaurant in Tahoe Keys East. For largemouth bass, management should begin prior to end of June or when average temperatures exceed 16 ºC (see below for more detailed report on bluegill).

In addition, the west shore seems to have the shortest suitable spawning period, followed by the north shore, then the east shore, with south lake having the longest overall suitable spawning period (Table 16). Number of suitable spawning days for both largemouth bass and bluegill show a slight decline in 2007 followed by an increase in 2008. However, the 2008 estimates were still shorter than the number of days in 2006 (Table 17).

As temperature appears to be an insignificant barrier to nearshore invasion, areas in the lake not yet invaded by fish but contain vegetation, including milfoil, should be first priority for monitoring sites for new warm-water fish populations. Figure 23 and Table 18 show milfoil nearshore distributions from 2006-2008 (Anderson 1996). Enclosed sites with vegetative substrate should be of higher priority than exposed sites with vegetation because the former experienced elevated summer temperatures. Regardless of substrate type, we found that enclosed sites were warmer than exposed nearshore sites approximately from May to October 2006, but cooled faster than pelagic and exposed nearshore waters near or during the first week in October. Figure 24 illustrates this by comparing the thermal regime in Tahoe Keys marina and a nearby non-marina exposed site, Timbercove, from May 2006 through Aug 2007. Similar temperature differences were also observed in 2008.

Based on observed dates for fish emergence at nearshore sites, we suggest that monitoring take place at least once in the middle of July and once at the end of August. The highest number of marina/embayment sites occupied by warm-water non-native species and native species occurred on July 10, 2006 (Figure 25). Bluegill seen at Lake Forest, an exposed site, from June 28 to August 14, 2006 accounted for the proportion of sites occupied by non-natives at non-marina sites (Figure 26).

Inferences about the movement of non-native fishes can be made from temperature data and snorkel sightings of adult largemouth bass in open water. In October 2006 a diver reported an adult size largemouth bass in open water near Caspian Point, approximately 30 m offshore. Two other sightings of largemouth bass were made; the first by a snorkeler at Camp Richardson marina in early July 2006, the second occurred 10 m offshore from Sand Harbor in the boat launch area on July 18, 2007 (Andrew Tucker, pers. communication). These sightings considered in isolation may be subject to question, but as the number of accounts build so does the case for mobile largemouth bass when marina temperatures climax in July, and when they begin to cool faster than pelagic water in October. Full quantification of movement patterns could be achieved via acoustic, radio, floy, or some combination of the three tags. In 2008, we used acoustic tags to track movements of bluegill and largemouth bass within and around Tahoe Keys Marina proper.

Table 16. Date when minimum spawning temperature was achieved for largemouth bass and bluegill based on daily average temperature taken at three-hour intervals. Values are listed clockwise around the lake from the Tahoe Keys. Shaded cells represent sites where no data were collected.

| | Date minimum spawning temperature reached | | | | | |
|---|---|---|---|---|---|---|
| | Largemouth bass | | | Bluegill | | |
| Site | 2006 | 2007 | 2008 | 2006 | 2007 | 2008 |
| Tahoe Keys Marina (East) | 14-May** | 27-May | 17-May | 20-Jun | 3-Jun | 15-Jun |
| Tahoe Keys Home (West) | 13-May** | 15-May | 14-May | 20-Jun | 28-May | 9-Jun |
| Taylor Creek | 18-Jun | 17-Jun* | 5-Aug** | 23-Jun | 17-Jun* | 5-Aug** |
| Emerald Bay | 20-Jun | 14-Jun* | 5-Aug** | 22-Jun | 6-Jul* | 5-Aug** |
| Meeks Bay | 22-Jun | 16-Jun | | 9-Jul | 5-Jul | |
| Obexers | 23-Jun | 5-Jul | 7-Jul | 9-Jul | 16-Jul | 9-Jul |
| Sunnyside | 23-Jun | 4-Jul | 6-Jul | 15-Jul | 23-Jul | 8-Jul |
| Tahoe City Marina | 19-Jun | 4-Jul | 28-Jun | 24-Jun | 10-Jul | 9-Jul |
| Tahoe City Non Marina | 29-Jun* | | | 29-Jun* | | |
| Lake Forest | 20-Jun | | | 26-Jun | | |
| Star Harbor | | 15-Jun | 24-Jun | | 5-Jul | 7-Jul |
| Carnelian Bay | 18-Jun | 19-Jun | 24-Jun | 24-Jun | 6-Jul | 2-Jul |
| Crystal Bay | 6-Jun | 16-Jun* | 20-Jun | 22-Jun | 17-Jun* | 28-Jun |
| Sand Harbor | 17-Jun | 15-Jun | 20-Jun | 24-Jun | 19-Jul* | 26-Jun |
| Sand Point | 16-Jun | 14-Jun | 24-Jun | 25-Jun | 4-Jul | 27-Jun |
| Cave Rock | 21-Jun | 17-Jun | | 1-Jul | 7-Jul | |
| Zephyr Cove | 8-Jun | 15-Jun | 17-Jun | 25-Jun | 6-Jul | 30-Jun |
| Elk Point | | 3-Jun | 16-Jun | | 17-Jun | 30-Jun |
| Round Hill Pines | 19-Jun | 15-Jun | 16-Jun | 30-Jun | 6-Jul | 30-Jun |
| Lakeside | 8-Jun | 12-Jun | 27-Jun | 25-Jun | 16-Jun | 27-Jun |
| Ski Run | 17-Jun | 12-Jun | 18-Jul** | 21-Jun | 15-Jun | 18-Jul** |
| Timbercove | 13-May | 21-Jun | 8-Jun | 21-Jun | 21-Jun | 15-Jun |

* Probe failure during sampling period. It is likely minimum temperature was reached prior to the indicated date and number of days above minimum spawning temperature is greater.
** First recorded temperature was minimum spawning temperature, therefore earlier minimum spawning temperature than detected is possible.

Table 17. Number of days that minimum spawning temperature was achieved for largemouth bass and bluegill based on daily average temperature taken at three-hour intervals. Values are listed clockwise around the lake from the Tahoe Keys.

| | No. of days above minimum spawning temperature | | | | | |
|---|---|---|---|---|---|---|
| | Largemouth bass | | | Bluegill | | |
| Site | 2006 | 2007 | 2008 | 2006 | 2007 | 2008 |
| Tahoe Keys Marina (East) | 129** | 116 | 104 | 87 | 102 | 86 |
| Tahoe Keys Home (West) | 129** | 124 | 118* | 87 | 109 | 100 |
| Taylor Creek | 88 | 89* | 44* | 83 | 87* | 40* |
| Emerald Bay | 98 | 104 | 64* | 89 | 74 | 45* |
| Meeks Bay | 89 | 92 | | 67 | 69 | |
| Obexers | 88 | 78 | 87 | 67 | 59 | 52 |
| Sunnyside | 88 | 76 | 96 | 61 | 52 | 72 |
| Tahoe City Marina | 95 | 77 | 96 | 83 | 65 | 69 |
| Tahoe City Non Marina | 96* | | | 78* | | |
| Lake Forest | 102 | | | 81 | | |
| Star Harbor | | 79 | 67* | | 69 | 54* |
| Carnelian Bay | 104 | 94 | 100 | 83 | 88 | 76 |
| Crystal Bay | 116 | 98* | 104 | 89 | 93* | 92 |
| Sand Harbor | 96 | 101 | 26*** | 82 | 63* | 20*** |
| Sand Point | 111 | 100 | 105 | 85 | 75 | 83 |
| Cave Rock | 104 | 89* | | 139 | 65* | |
| Zephyr Cove | 121 | 65* | 108 | 82 | 44* | 77 |
| Elk Point | | 107 | 95 | | 70 | 70 |
| Round Hill Pines | 103 | 98 | 108 | 77 | 73 | 77 |
| Lakeside | 103 | 98 | 84 | 81 | 85 | 80 |
| Ski Run | 106 | 112 | 62* | 86 | 89 | 52* |
| Timbercove | 130 | 111 | 115 | 86 | 78 | 86* |

* Probe failure during sampling period. It is likely minimum temperature was reached prior to or after the indicated date and number of days above minimum spawning temperature is greater.
** First recorded temperature was minimum spawning temperature, therefore earlier minimum spawning temperature than detected is possible.
*** Probe was not replaced after reported missing on July 17, 2008

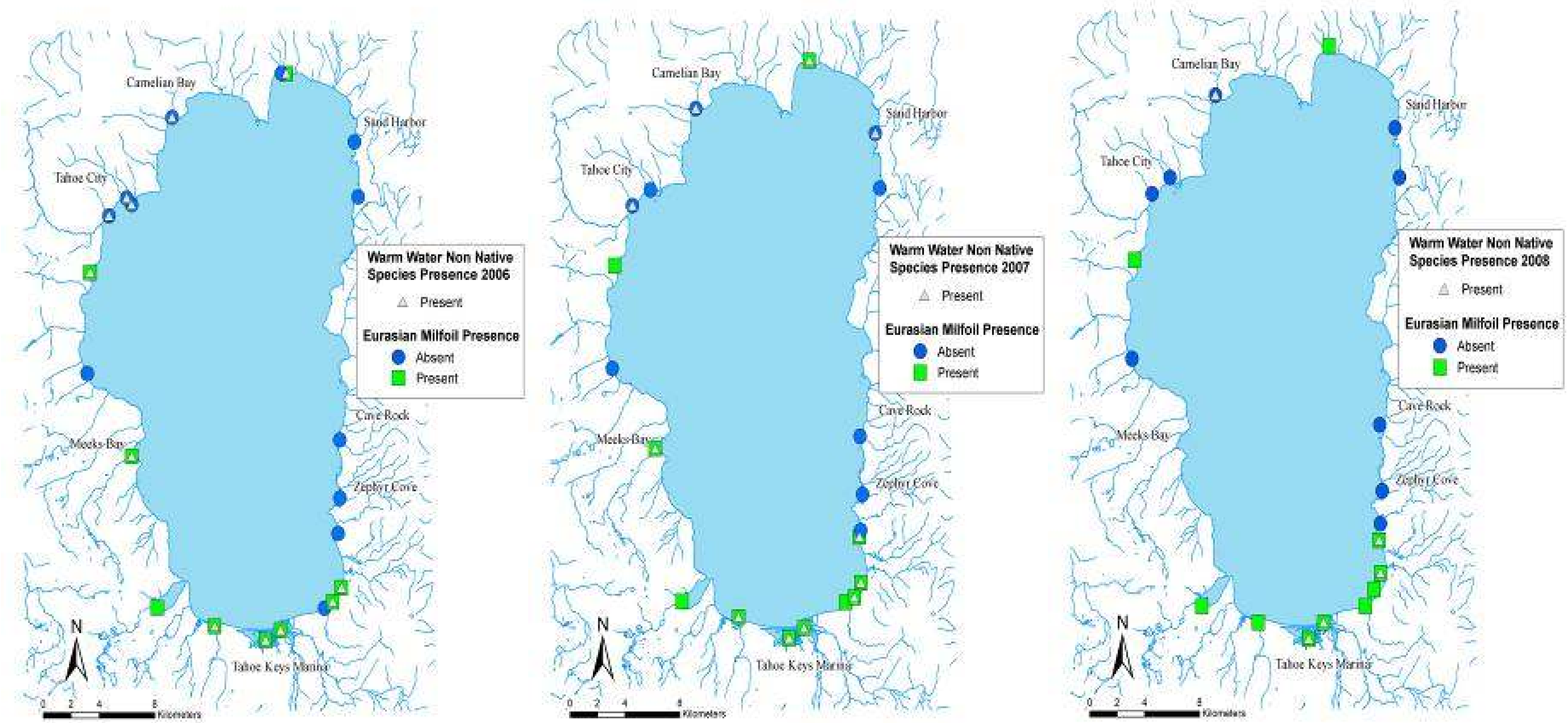


Figure 23. Distribution of warm-water non-native species and known populations of milfoil in the littoral zone. This includes particularly non-native strains of milfoil but some sites shown here contain other types of vegetation or native and hybrid milfoil strains.

Table 18. Bluegill, largemouth, and milfoil presence or absence during May-Nov 2006. Milfoil distribution data provided by Lars Andersen (USGS) from the 2006 Lake Tahoe Survey. Species presence is in bold type. *Sites not included in snorkel survey.

| | Species Presence (Yes/No) | | |
|---|---|---|---|
| Site | Bluegill | Largemouth | Milfoil |
| Lake Forest | **Y** | N | N |
| Star Harbor | **Y** | **Y** | N |
| Tahoe City | **Y** | **Y** | **Y** |
| Sunnyside | N | **Y** | **Y** |
| Obexer | N | N | N |
| Meeks Bay | **Y** | **Y** | **Y** |
| Emerald Bay | N | N | **Y** |
| Taylor Creek | **Y** | **Y** | **Y** |
| Tahoe Keys Marina | **Y** | **Y** | **Y** |
| Tahoe Keys Home | **Y** | **Y** | **Y** |
| Timbercove | N | N | N |
| Ski Run | **Y** | **Y** | **Y** |
| Lakeside | **Y** | **Y** | **Y** |
| Elk Point | **Y** | **Y** | **Y** |
| Round Hill Pines | N | N | N |
| Zephyr Cove | N | N | N |
| Cave Rock | N | N | N |
| Sand Point | N | N | N |
| Sand Harbor | N | N | N |
| Crystal Bay | **Y** | **Y** | **Y** |
| Carnelian Bay | **Y** | **Y** | N |
| *Tahoe Tavern | -- | -- | **Y** |
| *Logan Shoals Marina | -- | -- | **Y** |
| *Camp Richardson | -- | -- | **Y** |

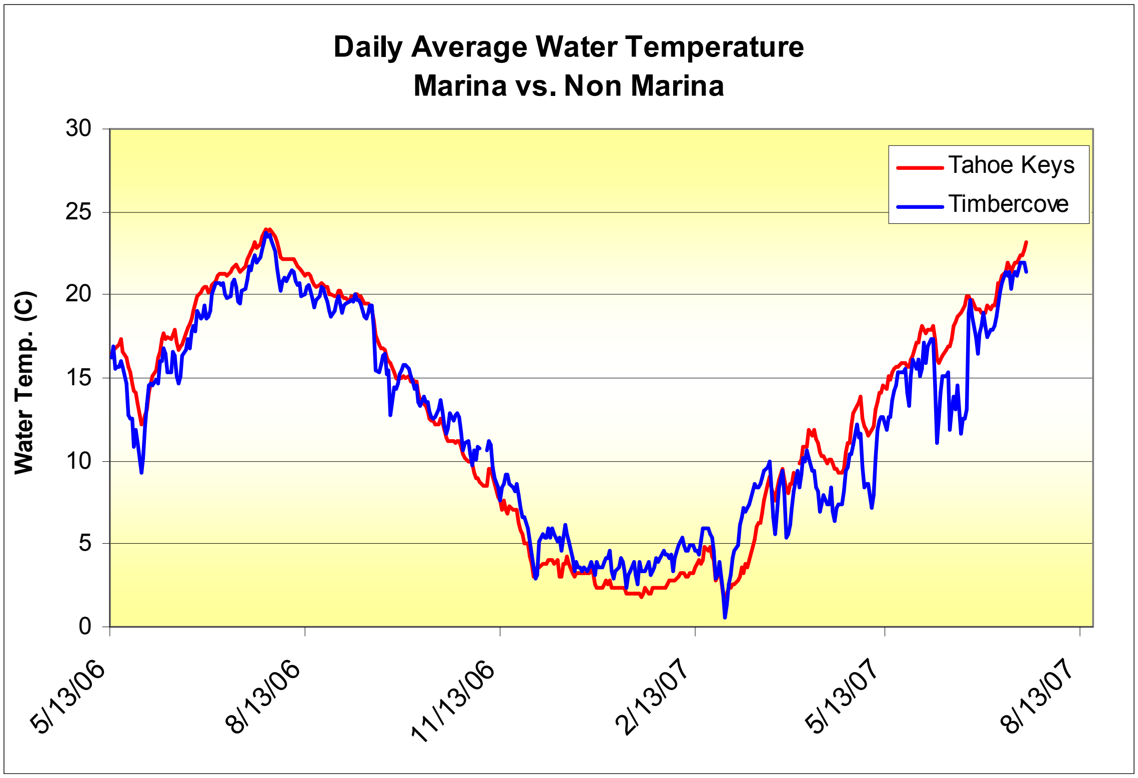


Figure 24. Daily average SWT of a marina site in the Tahoe Keys compared to its respective non-marina site, Timbercove from 13 May 2006 to 13 Aug 2007

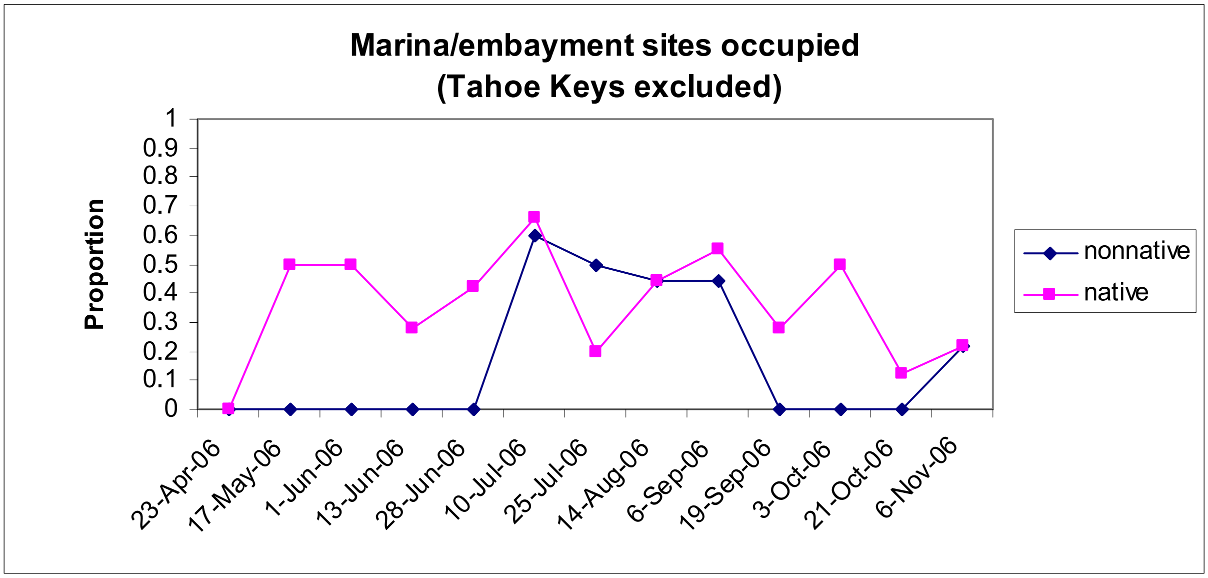


Figure 25. Proportion of marina or embayment snorkel survey sites, excluding Tahoe Keys, occupied by non-native and native fishes during the May to Nov 2006 snorkel survey period.

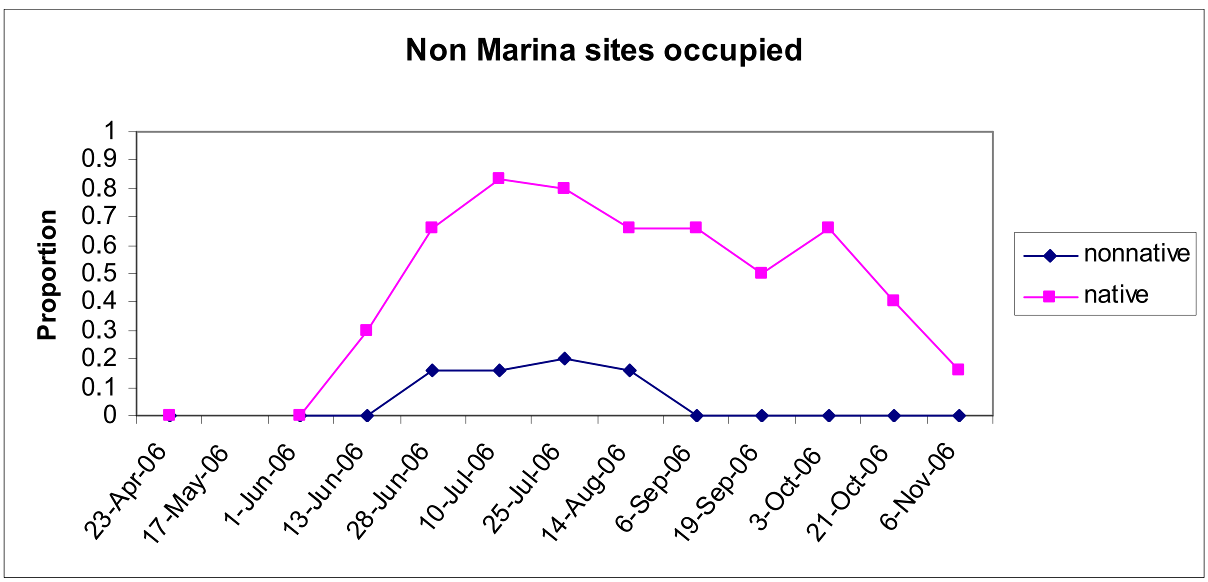


Figure 26. Proportion of non-marina sites occupied by non-native and native fishes during the May to Nov 2006 snorkel survey period.

*Warm-water non-native movements*

The acoustic receiver placed at Taylor Creek was missing when we sampled the site on August 7, 2008. We found no detection at Taylor Creek prior to that date. In addition, no detection was recorded by the outer west channel receiver during the course of our study. The receiver placed at the inner east channel was found semi-exposed (out of water) during our last sampling on December 3, 2008. We found fish that were detected by other receivers entering the Marina from the lake or leaving the Marina were not detected by the inner east channel receiver between October 23 and December 3. We believed that exposure of the receiver may have lead to its failure to detect passing fish, thus any detections during this time period by the outer east channel receiver were considered as a channel visit and implied a possible detection by the inner east channel receiver in our analysis.

Number of detections by our remaining seven receivers ranges from 44-3355 for BLUEGILL and 5423-48546 for largemouth bass. In order to facilitate and simplify interpretation of the massive amount of data collected, we established and defined several criteria for analysis. These criteria are listing in the following section.

*Temporal interpretation:*

The east section of the Marina where seven of the eight receivers were placed was divided into three sections: inner, middle, and outer east Marina. We classified each receiver into the three sections based on its location.

- Inner: Marina Cove (102119) and gas dock (102118)
- Middle: Sailing lagoon (102121) and inner east channel (102116)
- Outer: outer east channel (102122), 3$^{rd}$ red buoy (102120), and outermost green buoy (102110)

*Fish movement interpretation*:

a) Tag failure: no detection ever recorded by any receiver after deployment

b) Mortality: Fish that were no longer detected by any of our receivers prior to termination of our study (not including fish that are suspected to have moved out of the Marina). Explanations for such observation can be, but not limited to: loss of transmitter, movement, or death outside of all receiver detection range, as well as capture by anglers.

c) Inactive: Fish remaining at the same location for an extended period of time. Explanations for such observation can be, but not limited to: loss of transmitter or death within receivers' detection range, resting, spawning or nest guarding.

d) Moved out: Fish that were last detected in the outer section of the Marina with no subsequent detections within the Marina.

There were no inactive fish among our seven tagged bluegill. Mortality among our tagged bluegill was approximately 70% (5/7 individuals). Two of these fish were last detected at the inner section of the Marina, around our gas dock receiver. There are sections of the east Marina that were not covered by our receivers; therefore it is possible that the tagged fish were residing in these areas, hence their disappearance inside the Marina. Two other of these bluegill were last detected at the outer edge of the middle section of the Marina (inner east channel). Detection records suggest that the remaining 30 % (2/7 individuals: 7611 and 7613) of tagged bluegill may have moved out of the Marina as their last detected locations were at the outer section of the Marina and no further detections within the Marina were found thereafter. Figures 27 and 28 show the activities of these two tagged fish prior to their potential departure from the east Marina. Bluegill-7613 was found residing in the east channel before detection by the red buoy receiver (July 29) and then disappeared thereafter (Figure 27). Bluegill-7611 was last found residing at the outer east channel receiver before disappearing (Nov 27) (Figure 28). One should note that there is also another feasible explanation for the disappearance of bluegill-7611. The tagged fish could also have moved back into the Marina after detection by the outer east channel. Since the inner east channel receiver was not functioning properly and the Sailing lagoon receiver has already been taken out of the water due to low water level during that time period (Oct 23- Dec 3), the tagged bluegill could be residing at these out-of-range areas within the Marina and remain undetected.

For largemouth bass, there was one possible tag failure (13010). For the remaining 13 tagged largemouth bass, 40 % (5/13 individuals) were still in the Marina until the termination of our study on Dec 3. Among those 5 individuals, detections for three of the fish in the final week were mainly at the outer section of the Marina, whereas the other two were mainly residing at the inner section. Mortality among our tagged largemouth bass was approximately 40 % (5/13 individuals). Four individuals (13003, 13006, 13011, and 13013) had an extended period of inactivity prior to their disappearance in either early June or July. Half of them were last detected at the inner section of the Marina (Marina Cove) and the other half were last detected at the middle section of the Marina (Sailing Lagoon). Their "inactive" behavior may have been due to spawning. Water temperature in June and July at the Marina was suitable for spawning (≥16 ºC) for largemouth bass. One largemouth bass (13017) was last detected at the outer edge of the middle section of the Marina (inner east channel) prior to its disappearance in mid July. 20 % (3/13 individuals) of our tagged largemouth bass may have moved out of the Marina. Figures 29, 30 and 31 show the activity of these three tagged fish prior to their potential departure from east Marina. largemouth bass-13012 was last detected at the red buoy receiver (July 22; Figure 27). largemouth bass-13002 and 13014 were last detected at outer east channel prior to their disappearance on Nov 29 and 30 respectively (Figures 30 and 31). As bluegill-7611, these two largemouth bass could also have moved back into the Marina after detection by the outer east channel. Because the inner east channel receiver was not functioning properly and the Sailing lagoon receiver had already been taken out of the water due to low water level during that time period (Oct 23- Dec 3), the tagged largemouth bass could also have been residing at these out-of-range areas in the Marina remain undetected.

While we were downloading data from the receivers on June 24, 2008, three largemouth bass (~12-16 cm) were sighted around the receiver set beside the 3$^{rd}$ red buoy outside of the east Marina channel. This indicated that largemouth bass were moving outside of Tahoe Keys Marina.

We have also installed temperature loggers with the receivers to record daily water temperatures at our sampling sites in hopes of examining the possible relationship between movement of the fish and water temperature changes (Figure 32). Examining movements of the bluegill and largemouth bass that departed the Marina, we found that they either left late July or late November. Based on our water temperature record, late July was when water temperature within the Marina was the highest in the summer (~23 ºC) and late November was when water temperature within the Marina was reaching overwinter temperature (~5 ºC) (Figure 32).

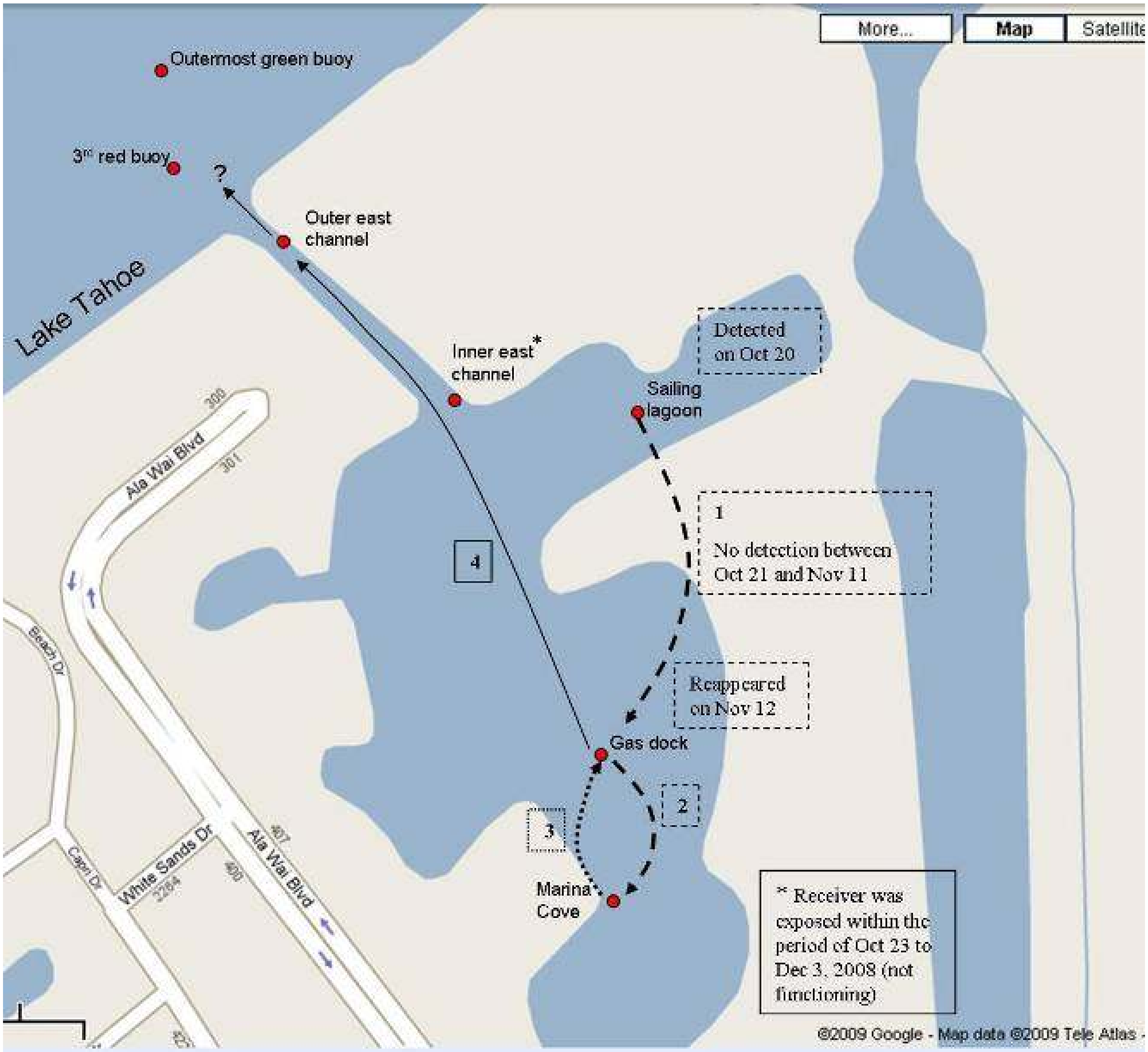


Figure 27. Activities of tagged bluegill 7611 (BG-7611) prior to its departure from the Marina. On Oct 20, BG-7611 was detected by the Sailing lagoon receiver. However between Oct 21 and Nov 11, it was not detected by any of our receivers (1). It then reappeared at the gas dock on Nov 12 and disappeared again in the same day. It reappeared on Nov 21 at the gas dock and moved to Marina Cove and possibly remained in the near-by area before returning to the gas dock on Nov 23 (2 and 3). It then remain undetected until the last detection at the outer east channel receiver on Nov 27, 2008 and thereafter it was no longer detected by any of our receivers until the termination of our study on Dec 3, 2008 (4). The base map of the Tahoe Keys Marina was obtained from Google© Map 2009.

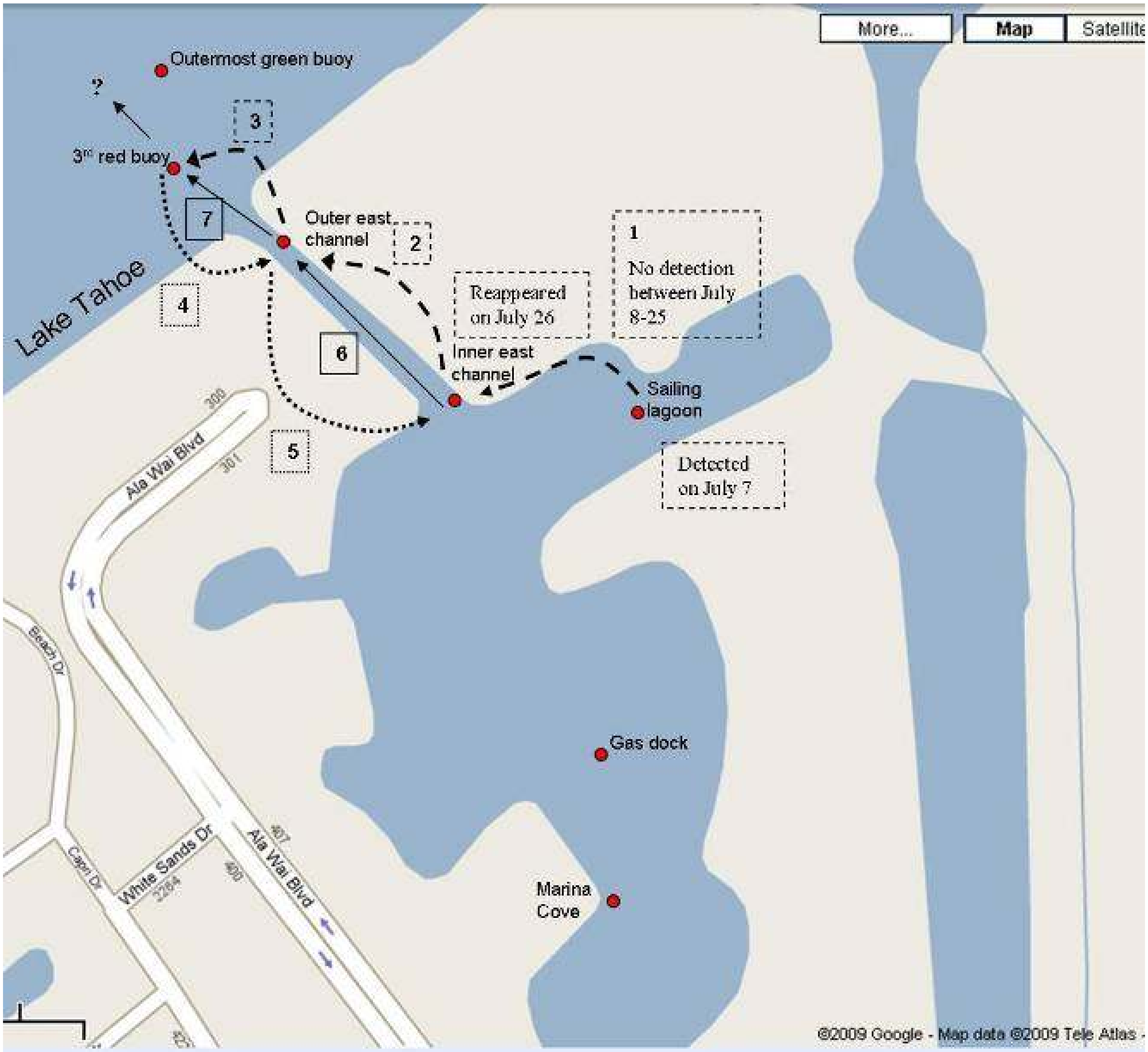


Figure 28. Activities of tagged bluegill 7613 (BG-7613) prior to its departure from the Marina. On July 7, BG-7613 was detected by the Sailing lagoon receiver. However between July 8 and 25, it was not detected by any of our receivers (1). It then reappeared at the inner east channel on July 26 and in the same day moved to the outer east channel and the 3rd red buoy (2 and 3). On July 28, it moved back into the channel briefly before returning to the 3rd red buoy and remained there until July 29 (4, 5, 6, and 7), and was then no longer detected by any of our receivers until the termination of our study on Dec 3, 2008. The base map of the Tahoe Keys Marina was obtained from Google© Map 2009.

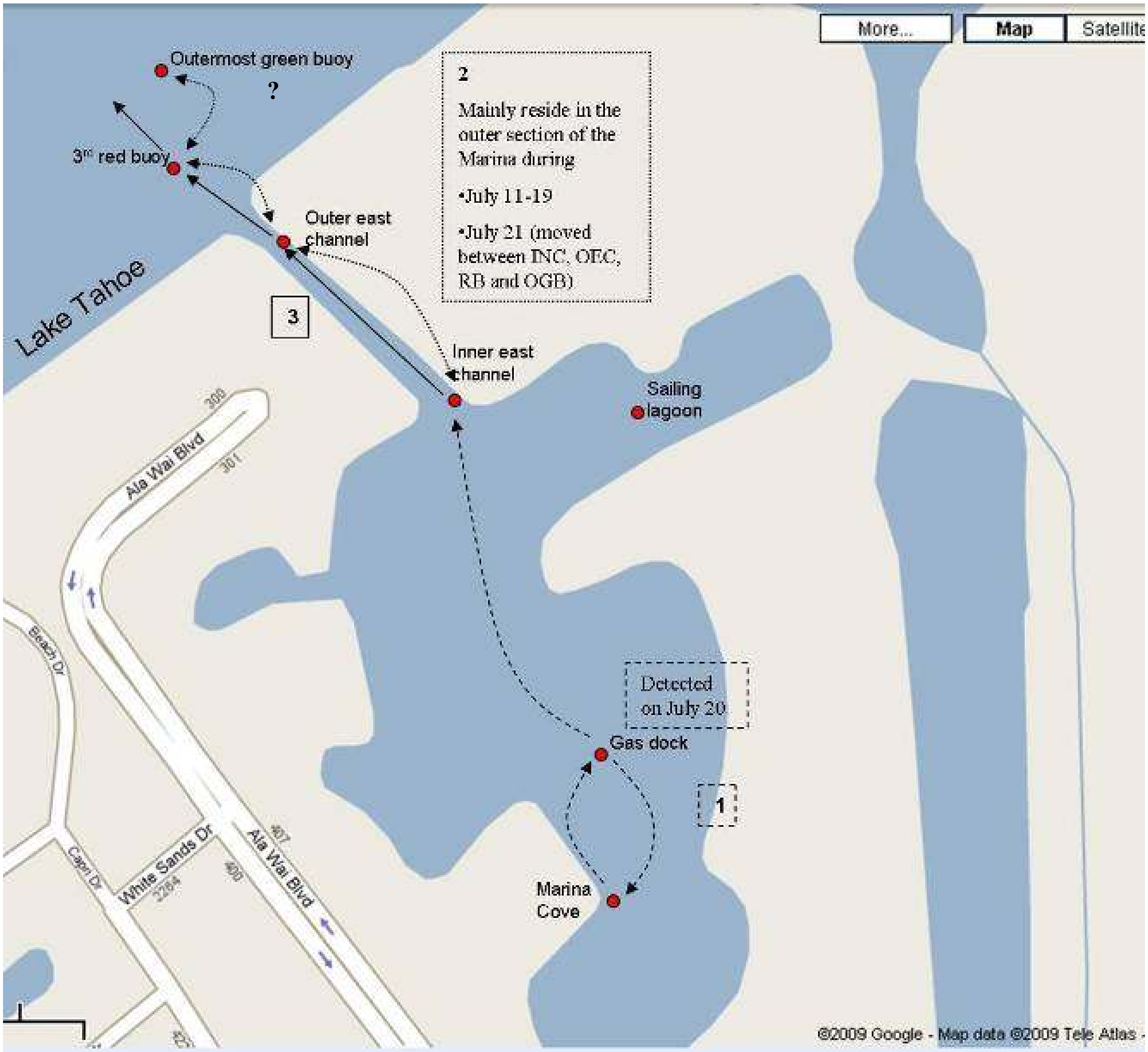


Figure 29. Activities of tagged largemouth bass 13012 (LMB-13012) prior to its departure from the Marina. From July 11-19, LMB-13012 was detected mainly in the outer section of the Marina (2). It then moved to the inner section of the Marina (1) and was residing there on July 20 before moving back to the outer section on July 21 (2). On July 22, it moved back into the channel briefly before returning to the 3rd red buoy and was then no longer detected by any of our receivers until the termination of our study on Dec 3, 2008 (3). The base map of the Tahoe Keys Marina was obtained from Google© Map 2009.

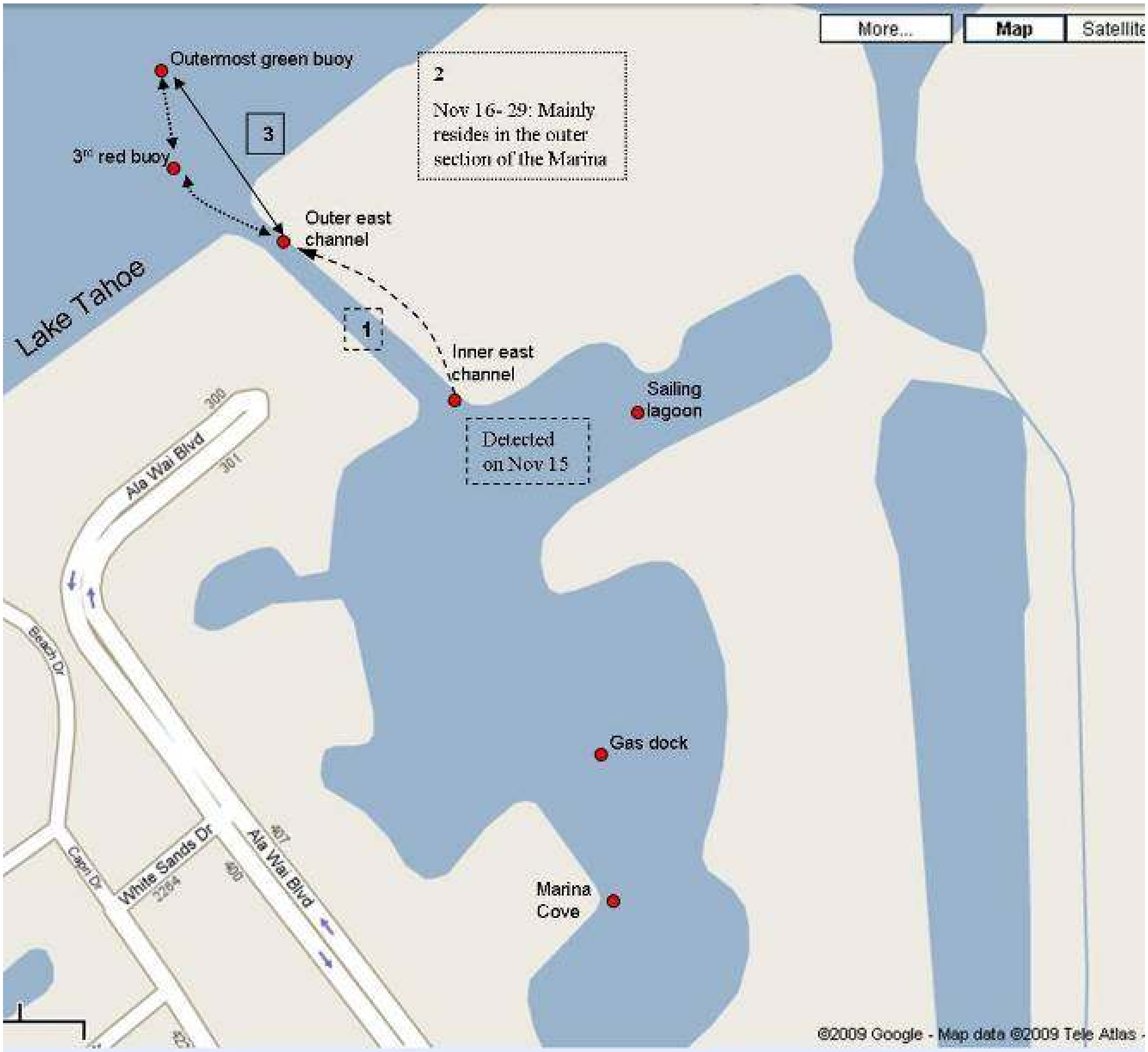


Figure 30. Activities of tagged largemouth bass 13002 (LMB-13002) prior to its departure from the Marina. On Nov 15, it was detected by the inner east channel receiver (1). Then, from Nov 16-28, it moved within the outer section of the Marina (2). On Nov 29, it moved from the outermost green buoy back to the opening of the channel and was then no longer detected by any of our receivers until the termination of our study on Dec 3, 2008 (3). The base map of the Tahoe Keys Marina was obtained from Google© Map 2009.

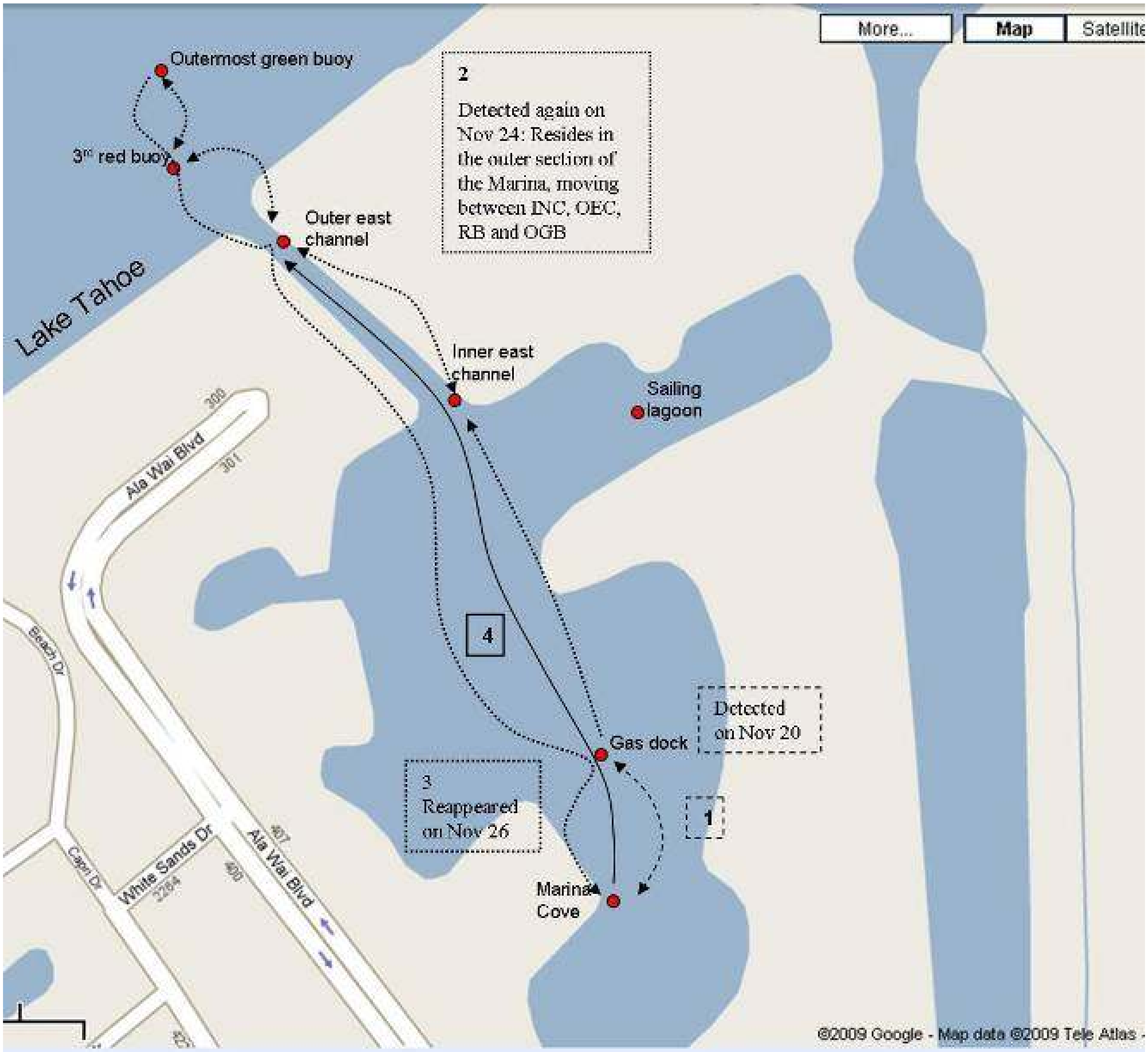


Figure 31. Activities of tagged largemouth bass 13014 (LMB-13014) prior to its departure from the Marina. On Nov 20, it was detected by the Gas dock receiver and was found residing in the inner section of the Marina before appearing at the outer section on Nov 24 (1 and 2). Then from Nov 26-28, it returned to the inner section (3). On Nov 30, it moved back to the channel and was then no longer detected by any of our receivers until the termination of our study on Dec 3, 2008 (4). The base map of the Tahoe Keys Marina was obtained from Google© Map 2009

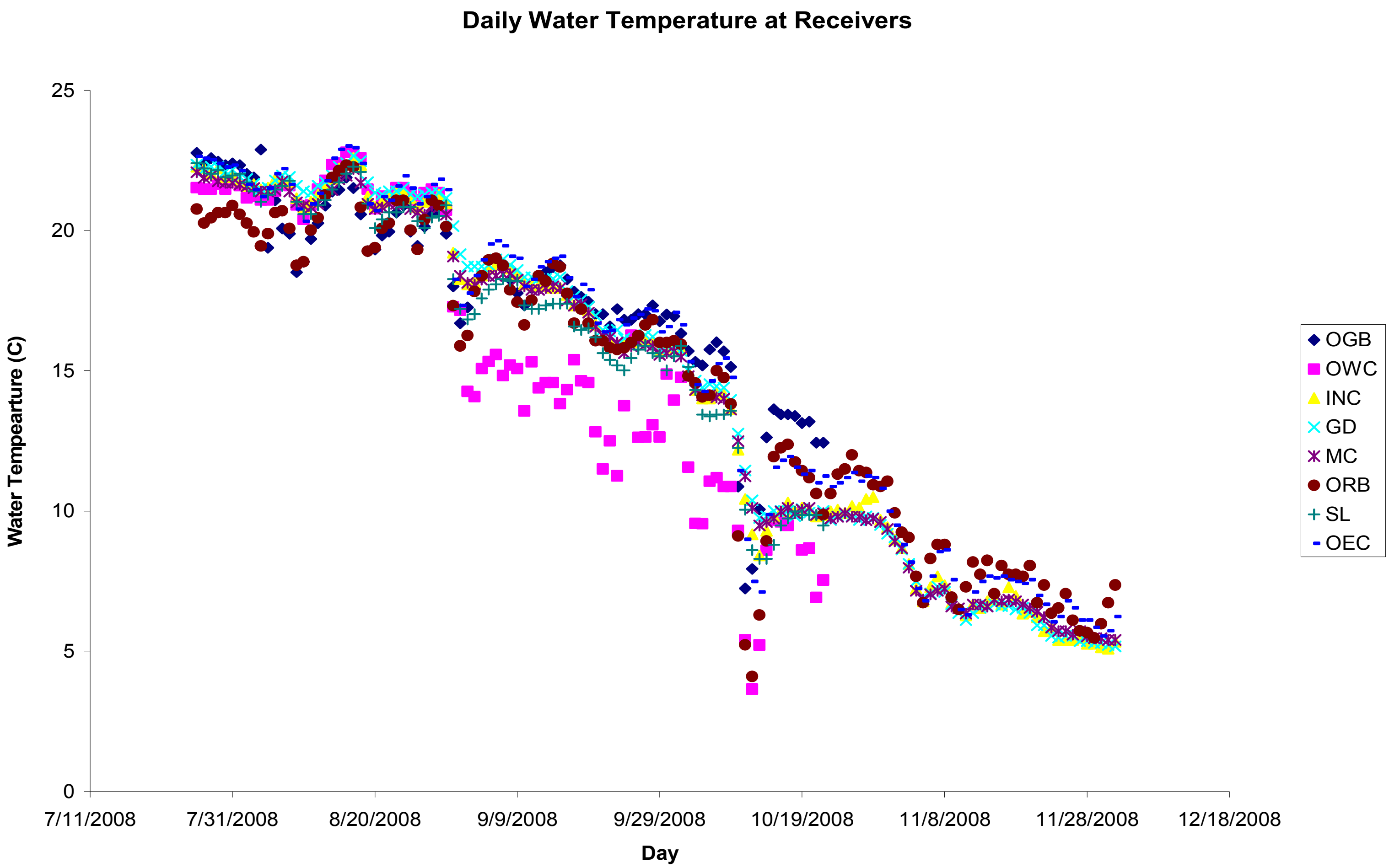


Figure 32. Daily surface water temperature between mid-July and early December 2008 at the eight receivers deployed within and around Tahoe Key Marina. DS1921Z-F50 i-button thermistors (Embedded Data Systems) were attached to each receiver to record daily water temperature at 3-hour intervals. OGB: Outermost green buoy 102110, OWC: Outer west channel 102114, INC: Inner east channel: 102116, GD: Gas dock 102118, MC: Marina Cove 102119, ORB: 3rd red buoy 102120, SL: Sailing lagoon 102121, and OEC: Outer east channel 102122. During sampling session on Oct 23, the outer west channel (OWC) receiver was found to be exposed due to low water level.

*Surface Water Temperature Model*

*Cluster analysis*

To facilitate partitioning and to minimize the effect of missing data, we performed cluster analyses with surface water temperature data from the time period that demonstrated greatest spatial and temporal variability in daily surface water temperature to identify thermally distinct regions within the lake. This period was chosen based on visual inspection of variation among the surface water temperature data. Combining the results from both analyses, we conclude that there is a consistent pattern in among-site, day-to-day temperature variations (both 2003 and 2006; Figures 33 and 34). The dendrogram of 2003 temperature from late spring to early summer period (Julian day: 158-195) shows that Tahoe Keys is thermally distinct from the other sampled sites (Figure 33). The dendrogram of 2006 surface water temperature from late spring to summer period (Julian day: 166-213) demonstrates similar results, with all sites from Tahoe Keys clustered together in one group that is itself more similar to the other south lake sites than it is to the remaining sites across the lake (Figure 34 and Table 19). When combined with visual inspection of the daily temperature regimes from all sampled sites, the plots from both 2003 and 2006 show that Tahoe Keys (TK) group is consistently warmer in late spring and early summer and cooler in autumn than the rest of the sampled sites (e.g. Figure 35 for 2003). The 2006 surface temperature plot (Figure 36) also shows that other south lake sites have warming and cooling rates intermediate to the TK group and all remaining sites. Sites located in other parts of the lake show both slower warming and slower cooling rates than the south lake sites.

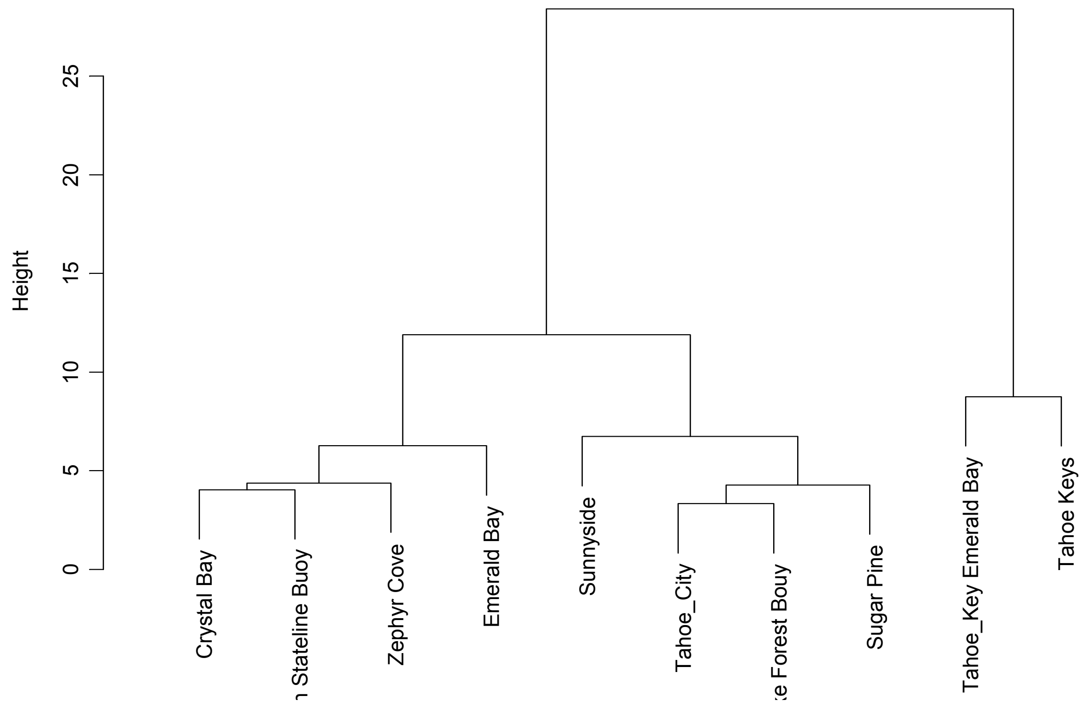


Figure 33. A dendrogram of 2003 late spring/early summer (Julian day:158-195) daily surface water temperature (SWT) of various sampled sites across Lake Tahoe based on Unweighted Pair-Group Means algorithm. The dissimilarity between sites in terms of daily SWT can be determined from the height at which various sites are joined into groups.

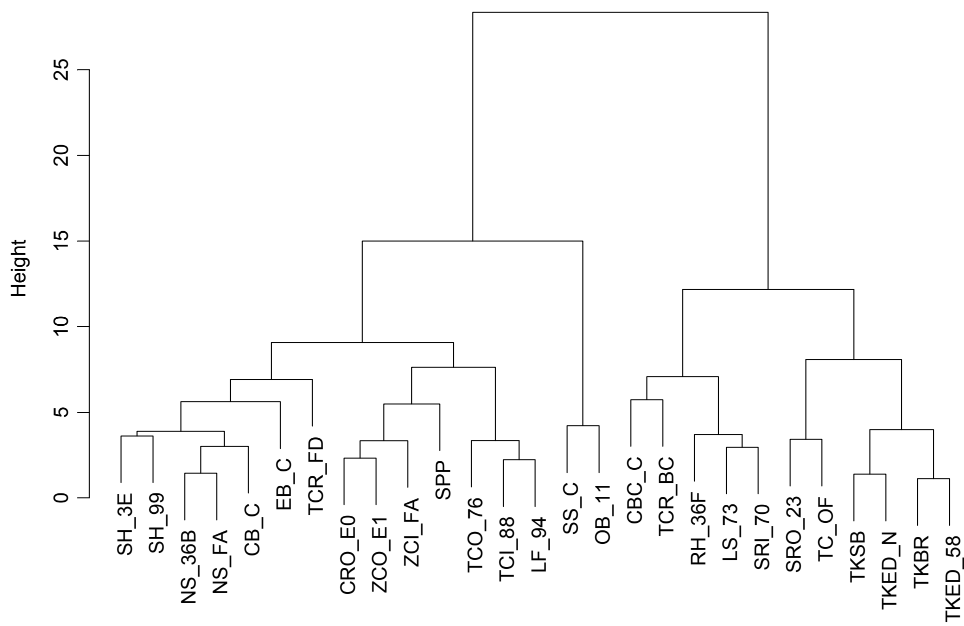


Figure 34. A dendrogram of 2006 late spring/early summer (Julian day:166-213) daily surface water temperature (SWT) of various sampled sites across Lake Tahoe based on complete linkage algorithm. Sample abbreviations denote sampling location and probe number. The dissimilarity between sites in terms of daily SWT can be determined from the height at which various sites are joined into groups.

Table 19. Codes of site names used in cluster analysis for 2006 and in Figure 36.

| Code for cluster analysis 2006 | Site Name |
|---|---|
| CB | Carnelian Bay |
| CBC | Crystal Bay Cove |
| CR | Cave Rock |
| EB | Emerald Bay |
| LF | Lake Forest |
| LS | Lakeside Marina |
| NS | Northern Stateline |
| OB | Obexers |
| RH | Roundhill Pine |
| SH | Sand Habour |
| SPP | Sugar Pine Point |
| SR | Ski Run Marina |
| SS | Sunnyside Marina |
| TC | Timber Cove |
| TCI/TCO* | Tahoe City |
| TCR | Taylor Creek |
| TK | Tahoe Keys |
| TKBR | Tahoe Keys Boat Rental |
| TKED | Tahoe Keys Emerald Drive |
| TKSB | Tahoe Keys Sheriff 's boat |
| ZC | Zephyr Cove |

* When acronyms has "I" at the end→ inshore probe, "O" at the end→ offshore probe

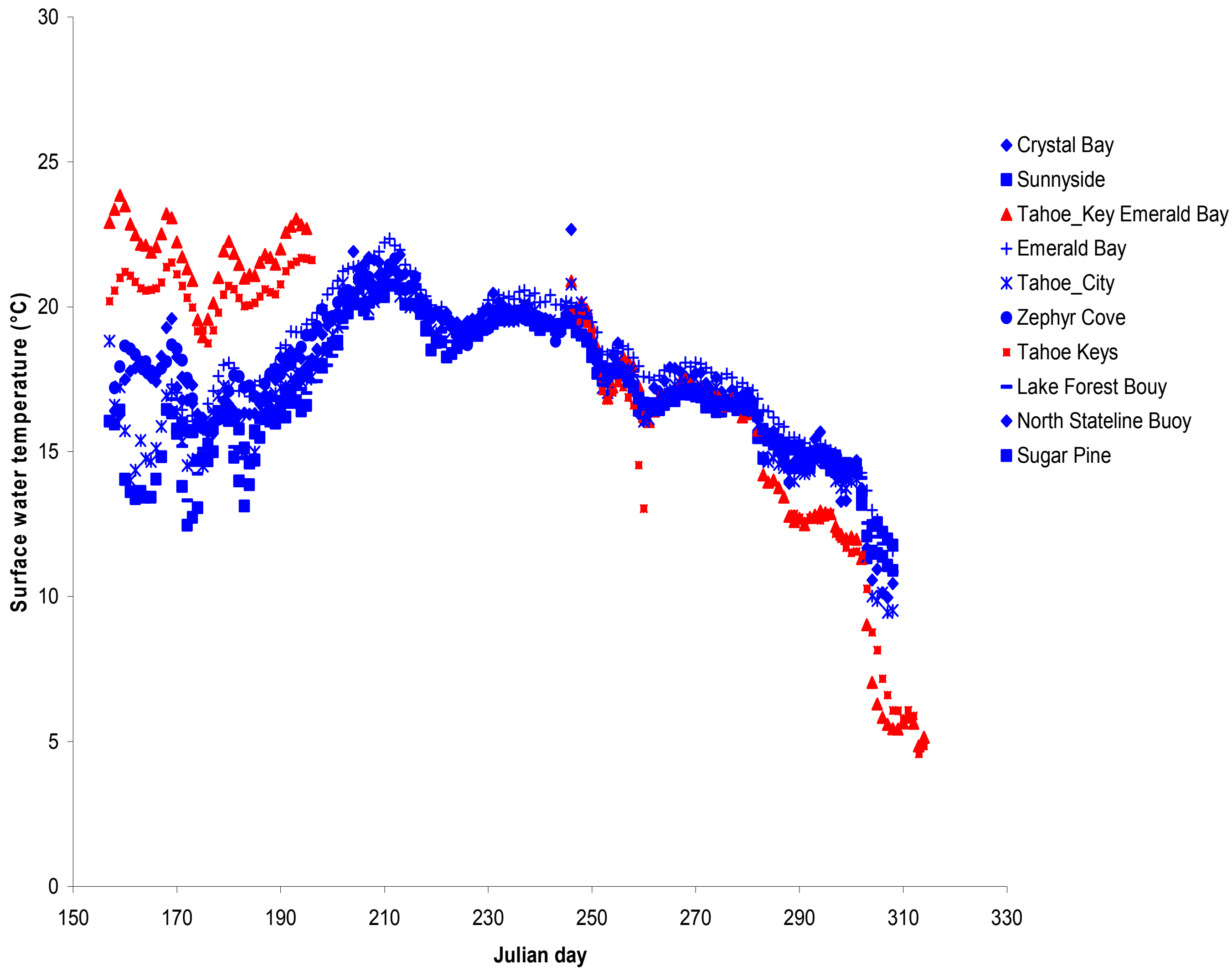


Figure 35. Daily surface water temperatures (°C) collected in 2003 from nearshore sites around Lake Tahoe.

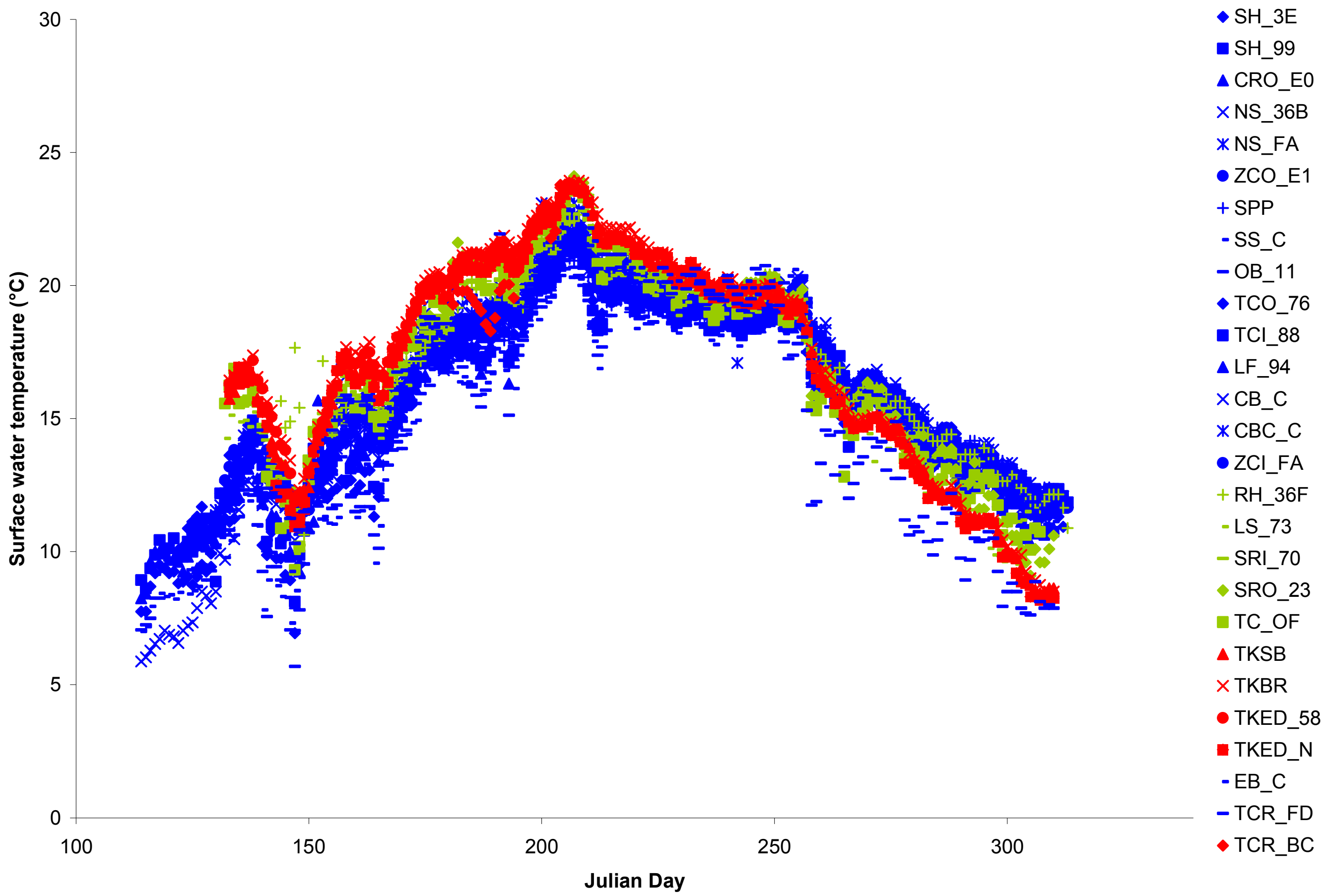


Figure 36. Color coded groups show distinct thermal regions were identified by cluster analysis in 2006. Warmest group is represented by the enclosed-site Tahoe Keys cluster (see Figure 32), other sites located in the south shore (RH, LS, SRI, SRO, & TC) seems to have intermediate warming and cooling rates. The remaining exposed sites have slower warming and cooling rates.

*Base and supplementary models*

Based on the results from cluster analysis, we developed two temperature predictive models for the warmest and coolest regions of the lake (See Method- Surface water temperature modeling). Using both the base and the supplementary model, we generated SWT projections for Tahoe's past, present and future for both thermal regions. Air temperatures input for the future projections were adopted from Snyder and Sloan (2005). The projections are limited to 2080 to 2099. The range of $CO_2$ concentration used for the future scenario was 635-686 ppm (Snyder and Sloan 2005). Figure 37 shows the past, present and future mean annual surface water temperature projections for the exposed sites. We projected an increase of approximately 1.5 °C in mean annual surface water temperature in the future under the Snyder and Sloan (2005) climate change scenario. For the enclosed sites, we calculated a 2 °C increase in mean annual temperature in the future and potential to extend suitable spawning period for warm-water invaders (Figure 37).

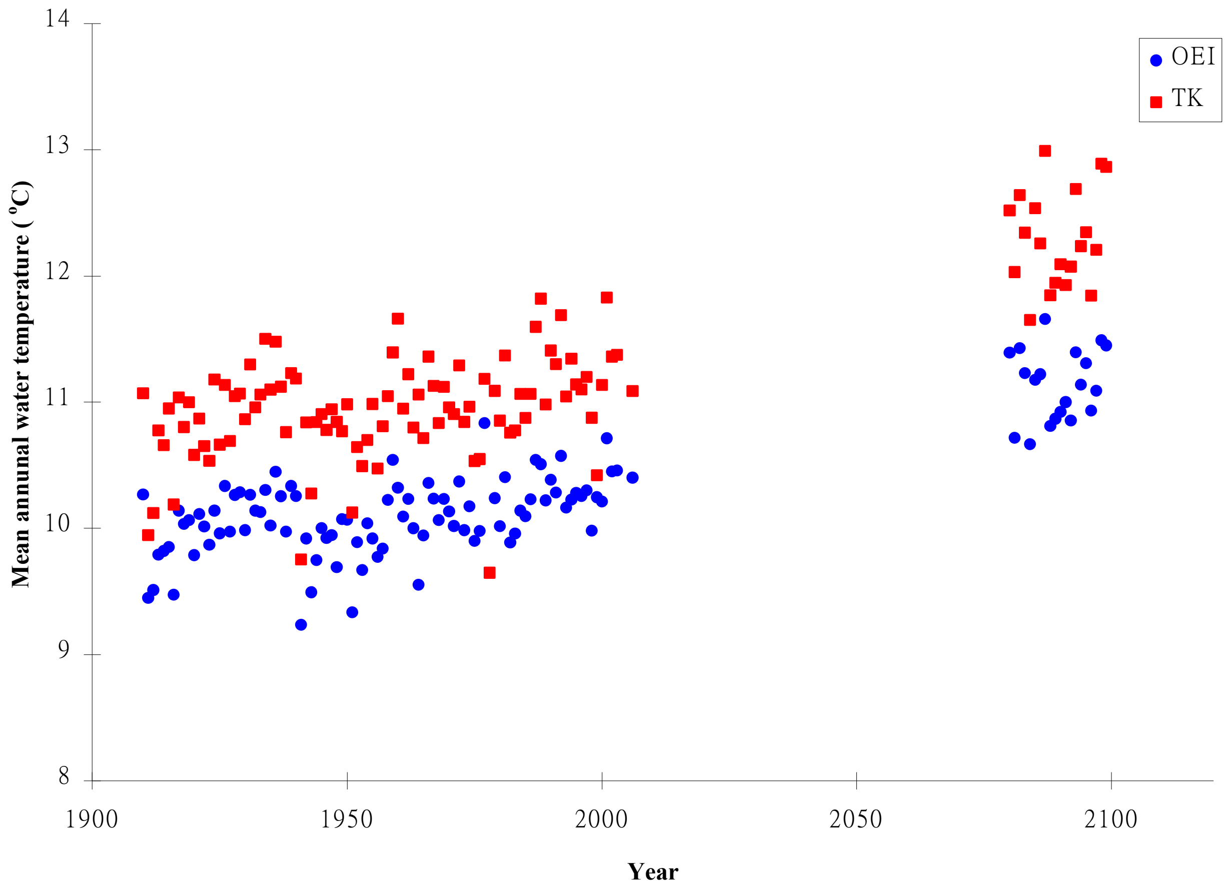


Figure 37. Past, present, and future mean annual surface water temperatures projections (°C) for exposed sites (OEI, blue circle) and enclosed sites (TK, red square) in Lake Tahoe.

*MODIS satellite temperature data: Predicting nearshore temperatures at many locations yet to be invaded*

Shallow-water nearshore temperatures fluctuate more widely than those of adjacent deep-water regions, with shallow water having lower temperature during cool conditions (winter/night) and correspondingly warmer temperatures during warm conditions (summer/day). However, the effects cancel each other in the mean. Therefore, weekly averages of both the MODIS and in situ temperatures were computed for 2006, to derive a predictive relationship for each site.

There was a strong correlation between offshore MODIS temperatures and nearshore thermistor temperatures. Least squares linear regression of the nearshore vs. offshore temperatures had high coefficients of determination ($r^2 \geq 0.90$), with one lower exception at the Emerald Bay site ($r^2 = 0.85$; Table 20). As a result, modeled nearshore temperatures based on MODIS remote sensing were used to calculate the potential spawning locations (layer 1) and consumption rates (layer 3) at each location.

Our novel method utilizing remote sensing of offshore temperatures to predict nearshore temperatures at our required spatial resolution was, to our knowledge, the first to provide a framework to remotely monitor Lake Tahoe's nearshore temperatures at high spatial resolution. High coefficients of determination ($r^2$) from offshore to nearshore temperature regressions indicate that remotely sensed offshore temperatures can effectively estimate and eventually monitor nearshore temperatures. Additionally, nearshore temperature estimates are validated from previous observations of thermal images (Steissberg et al. 2005). Nearshore temperatures in the northwest region (McKinney Bay) were consistently cooler than other lake regions. Thermal images confirmed upwelling cools the northwest region during the stratified period (Steissberg et al. 2005). In addition, Strub and Powell (1987) found that dominant surface gyres trapped warm water and nutrients in the northeast (Crystal Bay), and south portions of the lake; these same regions maintained the warmest thermal regimes in this study from May to October. Despite differences in temperature by region, all 50 nearshore sites were thermally suitable for at least two bass spawns, indicating spawning opportunity is not constrained by temperature. This result accords with Ngai (2008) whose results indicated the entire littoral zone was thermally suitable for bass growth.

Table 20. Coefficients of determination ($r^2$) and least squares linear regression equations from nearshore thermistor temperatures vs. offshore MODIS temperatures. Thermistors listed in clockwise order beginning at North Stateline, just west of Crystal Bay.

| Thermistor Site Location | Regression equation | $r^2$ |
|---|---|---|
| North Stateline | 0.8543x+ 2.4095 | 0.99 |
| Crystal Bay | 0.7295x+ 5.1627 | 0.96 |
| Sand Point | 0.8494x+ 2.2481 | 0.99 |
| Cave Rock | 0.7588x+ 4.1929 | 0.98 |
| Round Hill | 0.7854x+ 4.4937 | 0.97 |
| Zephyr Cove | 0.8248x+ 4.3089 | 0.90 |
| SkiRun | 0.8572x+ 3.0803 | 0.97 |
| Lakeside | 0.8187x+ 3.0171 | 0.95 |
| Timbercove | 0.8074x+ 3.5845 | 0.97 |
| Tahoe Keys Marina | 0.9094x+ 2.869 | 0.94 |
| Tahoe Keys Homeowner | 1.0679x - 0.1558 | 0.94 |
| Taylor Creek | 0.9975x+ 0.026 | 0.94 |
| Emerald Bay | 0.6296x+ 8.835 | 0.85 |
| Meeks Bay | 0.9480x+ 2.6186 | 0.90 |
| Obexers | 0.8189x+ 3.149 | 0.98 |
| Sunnyside | 0.8218x+ 2.7099 | 0.98 |
| Tahoe City | 0.8146x+ 3.8633 | 0.98 |
| Boatworks | 0.7896x+ 3.5751 | 0.99 |
| Lake Forest | 0.8463x+ 2.6631 | 0.99 |
| Carnelian Bay | 0.9670x+ 0.7178 | 0.96 |

*Suitable Spawning Locations (Layer 1) and Habitat (Layer 2) in the Nearshore*

One hundred percent of nearshore sites exceeded the minimum temperature required for bass spawning. Furthermore, all locations exhibited potential during the summer period for at least two spawns. In the 'suitable spawning location' layer, 56 % of sites maintained a thermal regime suitable for up to three spawns, and 44 % of locations allowed up to four spawns. Sites allowing up to four spawns were concentrated along the southwest, southeast, and northeast shoreline (Figure 38A). Emerald Bay maintained temperatures for up to five spawns, but was grouped with "up to four spawn" sites, as five spawns were deemed biologically unrealistic given photoperiod constraints. Aquatic vegetation was present at 30 % of the nearshore sites, and was continuously present along the south shore from Zephyr Cove to Taylor Creek. Patches of vegetation occurred throughout the remaining shoreline (Figure 38B).

While thermal requirements were met throughout the nearshore for spawning and growth, no sites approached optimal temperatures for bass growth (27.5 ˚C ± 2 ˚C) (Strawn 1961). Ecophysiological theory suggests fish pursue temperatures nearest their fundamental thermal niche for optimum feeding and growth (Magnuson et al. 1979). The establishment likelihood model assumed temperatures predict likelihood on the basis that spawning opportunity is governed by temperature (Coutant 1975, Rice et al. 1983). In addition bass recruitment should be high at the warmest sites where longer growing seasons for age-0 bass would decrease over-winter mortality (Post et al. 1998; Garvey et al. 2004). However, bass were only present in 44 % of the warmest sites identified by the model (up to four spawns). Given the limited variability among nearshore temperatures, it is likely that other factors, such as aquatic vegetation and food-availability, may provide benefits that outweigh those received from slightly warmer temperatures, and thus play a larger role in bass establishment.

Dominant wind patterns associated with warmer temperatures in the northeast and south could increase wind exposure on bass nests unless structures or vegetation are present to attenuate waves (Shirley and Andrews 1977). Therefore cooler habitats with aquatic vegetation present that reduces destructive wind exposure on nests may be preferable to the warmest sites. In fact when bass presence was compared to thermally suitable-spawning locations (layer 1) and habitat structure (layer 2) separately, habitat predicted current bass distribution with greater accuracy (Figure 38). This suggests that aquatic vegetation distribution currently limits bass establishment more than temperature. Distribution of preferred habitat type has been used in other intra-system predictive models with success; substrate classification reliably estimated *Dreissna* spp. densities in Lake Erie (Haltuch et al. 2000). Carlander (1975) found bass were commonly confined to vegetated areas in the littoral zone of large natural lakes, indicating that aquatic vegetation distribution may accurately delineate bass distributions in Lake Tahoe, and thus controlling the spread of aquatic vegetation could also control spread of warm-water non-native fishes.

As a result, shoreline areas with aquatic vegetation should be a high monitoring priority for preventing bass establishment, although this does not obviate monitoring at non-vegetated sites, which may have higher food-quality. Non-vegetated sites with high densities of native forage fishes (Beauchamp et al. 1994) would increase piscivory by bass, enhancing bass growth and over-winter survival (Post 2003). Littoral fish abundance has declined in the Tahoe Keys since 1992 (California Department of Fish and Game, unpublished observation, 1999), likely decreasing the proportion of fish in bass diets. Kamerath et al. (2008) suggests that warmwater fishes in Lake Tahoe are associated with reduced native fish abundance. If bass are depleting their prey base, then non-vegetated habitats with greater food-quality could enhance growth. For bass in Lake Tahoe trade-offs likely exist for achieving higher food-quality versus preferred habitat (vegetation), but our current model cannot decipher how prey base would impact site selection by bass.

*Layer 1 and Layer 2 Compared to Bass Presence*

Each of the model layers ('suitable spawning location' and 'habitat' layers combined) were compared to bass presence observed in 2006 as an indicator of the layer's ability to predict bass establishment. In 2006, bass were observed at 10 snorkel sites that coincided with 10 nearshore sites. Of these 10 sites, 40 % of them (4 sites) occurred in the areas with higher spawning potential (up to four spawns), and 60 % occurred in areas of lower potential (up to three spawns). When bass presence was compared to the habitat layer, 90 % of bass occurrence sites (9 sites) also contained aquatic vegetation, and 10 % of sites (1 site) did not contain vegetation (Figure 38).

*Establishment Likelihood Classification Compared to Bass Presence*

Layering 'suitable spawning location' and 'habitat' to classify likely bass establishment resulted in 18 % (9 sites) of the 50 nearshore sites identified as areas highly likely for bass establishment. Establishment was likely at 20 sites and least likely at 21 sites (Table 21; Figure 39). Bass were present in 44 % of 'highly likely' sites, 30 % of 'likely' sites, and 5 % of 'least likely' sites (Figure 40).

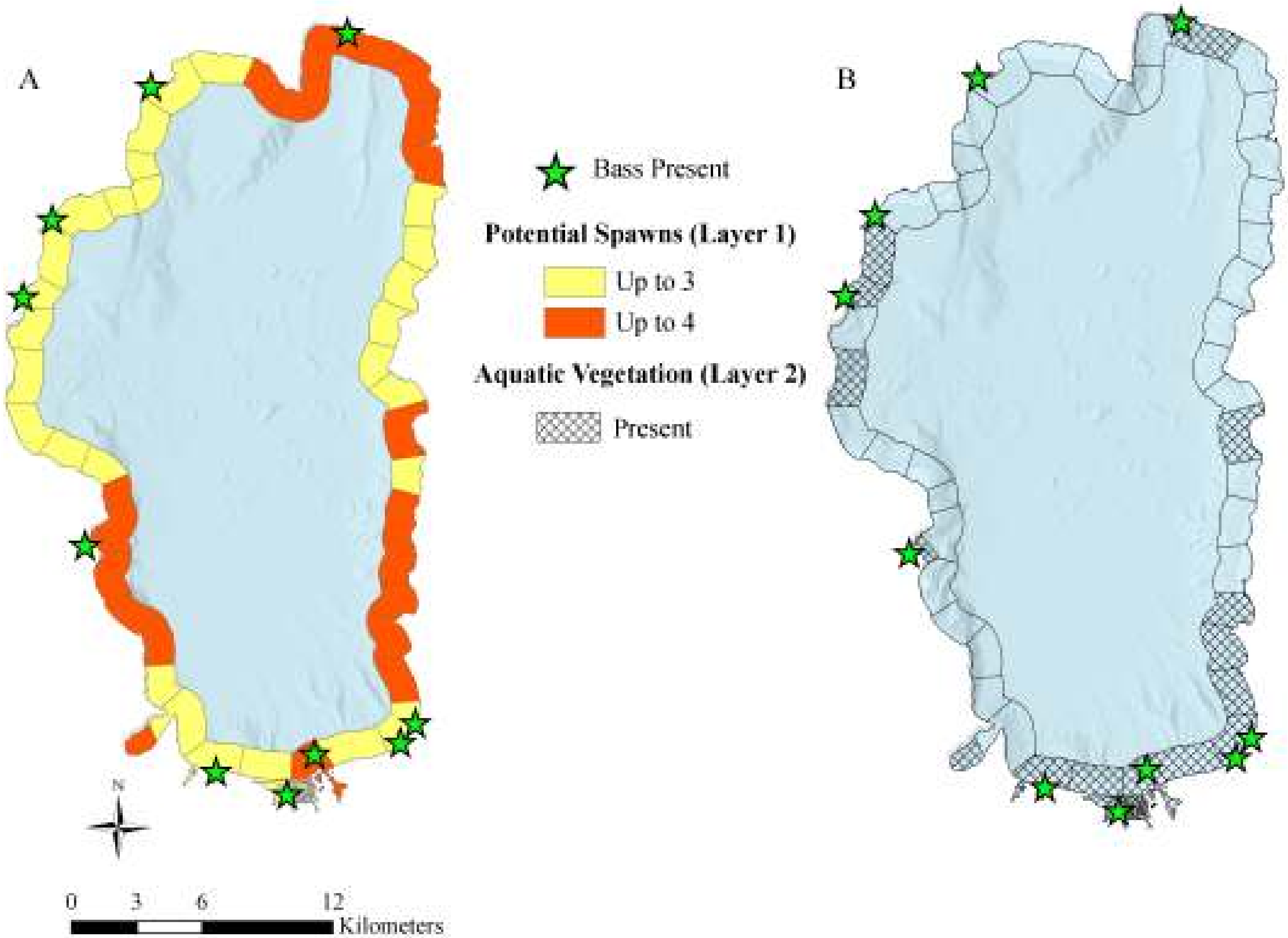


Figure 38. A) Layer 1, number of largemouth bass spawns possible, and B) layer 2, Presence of aquatic vegetation, compared to bass presence observed in 2006. All data observed, or estimated for May to October 2006. Bass were present in 2006 denoted by stars. The entire nearshore is thermally suitable for spawning and vegetation appears to limit bass more so than temperature.

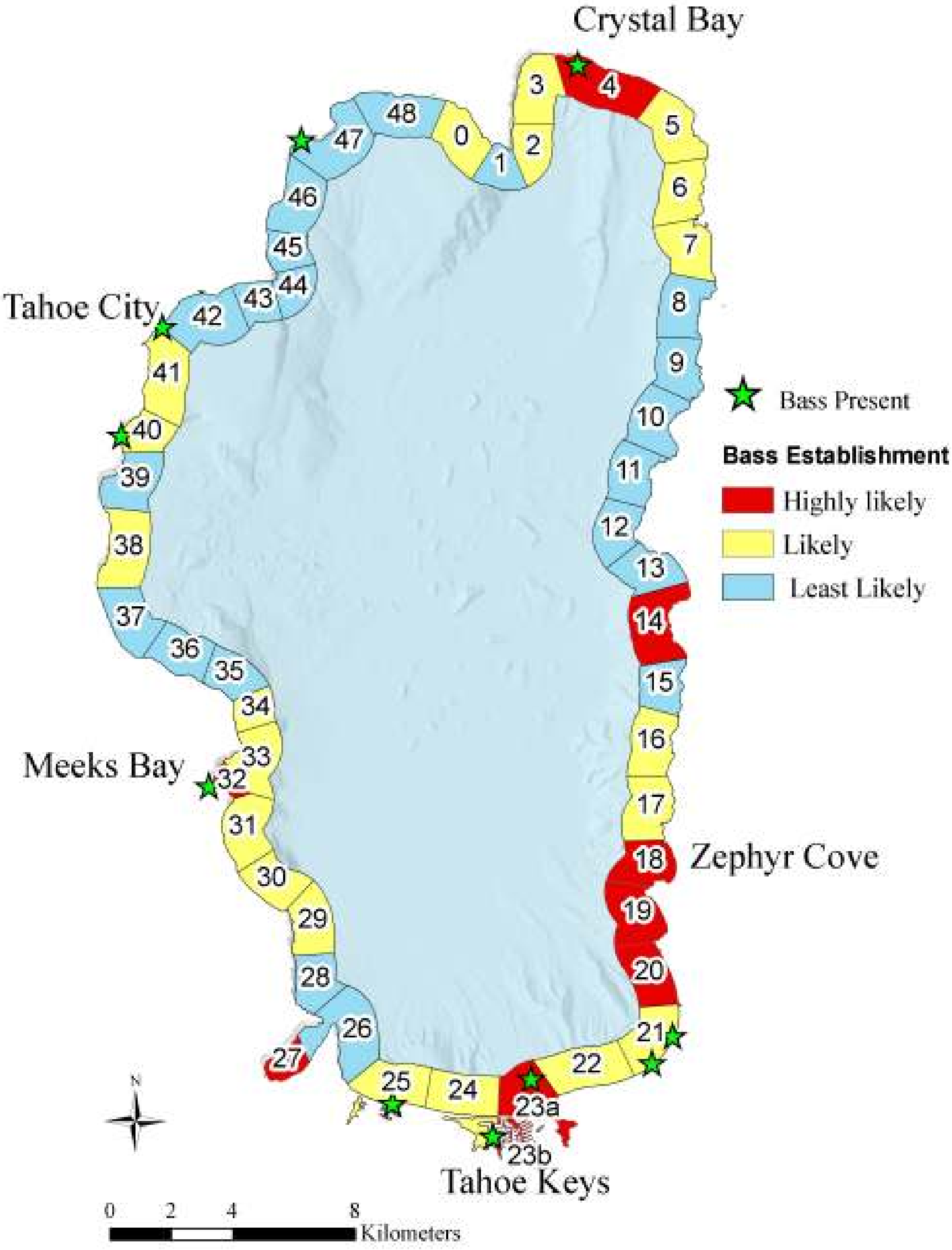


Figure 39. Layers 1 and 2 were combined to estimate likelihood of bass establishment which is shown for each nearshore site. Nearshore sites are labeled by number. Bass were present at 10 sites in 2006 and denoted with a star. The frequency at which bass were present within each level of establishment likelihood classification coincides with the rank of likelihood identified by the model.

Table 21. GPS locations (NAD 1983 Zone 10) of nearshore sites and designation for likelihood of bass establishment.

| Nearshore Site | Establishment Highly Likely |
|---|---|
| 4 | 762163.504644; 4347925.82323 |
| 14 | 763999.549171; 4329714.98159 |
| 18 | 764108.351809; 4321998.15445 |
| 19 | 763822.744883; 4320352.51454 |
| 20 | 763999.549171; 4318625.27265 |
| 27 | 750984.033526; 4315442.79547 |
| 32 | 748998.385371; 4324827.02305 |
| 23a | 759393.526; 4312978.6 |
| 23b | 759837.848244; 4313797.15556 |
| | **Likely** |
| 0 | 757906.601408; 4345872.17343 |
| 2 | 759089.830103; 4345450.5632 |
| 3 | 759076.229773; 4347014.60113 |
| 5 | 764774.767971; 4345953.7754 |
| 6 | 765033.174237; 4344199.33286 |
| 7 | 765400.383143; 4342172.88371 |
| 16 | 763958.748181; 4326219.69683 |
| 17 | 764067.55082; 4323643.79436 |
| 21 | 764203.554118; 4316231.6146 |
| 22 | 761265.882875; 4314817.1803 |
| 24 | 757104.181948; 4313919.55853 |
| 25 | 755077.732804; 4314259.56678 |
| 29 | 751786.452986; 4320039.70695 |
| 30 | 751038.434845; 4320746.9241 |
| 31 | 749515.197905; 4323154.18248 |
| 33 | 750208.814726; 4325792.64647 |
| 34 | 749868.80648; 4326894.27319 |
| 38 | 745856.709181; 4332402.40677 |
| 40 | 746101.515118; 4336055.45536 |
| 41 | 747121.539855; 4338068.30417 |
| | **Least Likely** |
| | 758790.622847; 4345328.16023 |
| 8 | 765005.973578; 4340119.23391 |
| 9 | 764910.771269; 4338310.39004 |
| 10 | 763985.948841; 4336311.14156 |
| 11 | 763278.73169; 4334638.30099 |
| 12 | 762829.920805; 4332843.05745 |
| 13 | 763319.532679; 4332231.04261 |
| 15 | 764339.557416; 4327647.73146 |
| 26 | 753309.689927; 4316435.61955 |
| 28 | 751908.855954; 4318040.45847 |
| 35 | 749515.197905; 4327737.49363 |
| 36 | 748100.763603; 4328240.70584 |
| 37 | 745897.510171; 4329750.34245 |
| 39 | 746128.715778; 4334904.86745 |
| 42 | 748892.302799; 4340170.91516 |
| 43 | 750932.352273; 4341000.53528 |
| 44 | 751258.760189; 4341095.73759 |
| 45 | 751136.35722; 4341626.15045 |
| 46 | 751530.766785; 4343815.80356 |
| 47 | 752986.002077; 4345851.77293 |
| 48 | 755202.855838; 4347048.60196 |

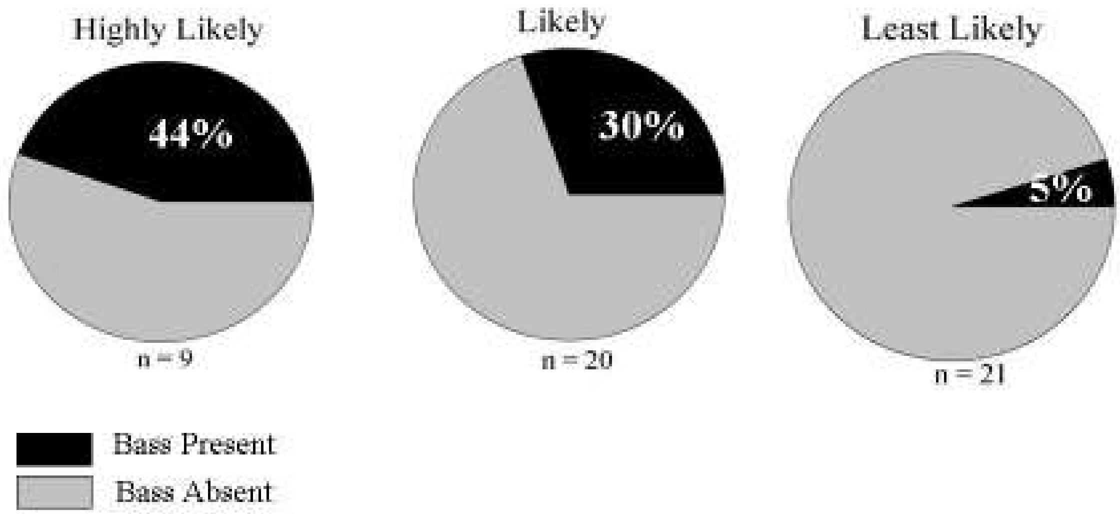


Figure 40. For each of the three classifications of bass establishment likelihood, the percentage of those sites that contained bass in 2006 are shown and denoted by the black pie piece in each chart. The frequency that bass were present within each site classification is proportional to the rank of likelihood.

*Tahoe Keys Consumption by Bass*

The mean proportionality constant, P (proportion of maximum consumption achieved), across cohorts was $0.41 \pm 0.09$. Thus an average fish in the Tahoe Keys is feeding at 41 % of its maximum possible consumption rate in order to achieve the growth required to grow from the start weight to end weight inputs. Maintenance rations for cohorts 1 through 8 exceeded consumption rates in the Tahoe Keys in May and October indicating negative growth occurred in these months (Table 22).

Consumption per unit of body weight declined with age. Mean consumption rates of an individual bass across 50 nearshore sites ranged from $2.4 \pm 0.8$ % body weight$\cdot d^{-1}$ for cohort 1 to $0.6 \pm 0.2$ % body weight$\cdot d^{-1}$ for cohort 8 (Figure 41).

Table 22. Maintenance rations in % body weight·d$^{-1}$ (amount consumed to maintain current weight) were iteratively calculated for each bass cohort and compared to consumption rates (% body weight·d$^{-1}$) estimated for each month. All values were estimated using the Wisconsin model. *Maintenance requirements exceed consumption rates resulting in negative growth for all cohorts during May and October.

| | | Consumption Rate (% body weight · d$^{-1}$) | | | |
|---|---|---|---|---|---|
| Age | Maintenance Ration (% body weight · d$^{-1}$) | May | June | Aug | Oct |
| 1 | 1.87 | 1.42* | 2.41 | 3.06 | 1.43* |
| 2 | 1.37 | 1.08* | 1.80 | 2.23 | 1.12* |
| 3 | 1.27 | 1.03* | 1.73 | 2.23 | 1.12* |
| 4 | 0.81 | 0.63* | 1.08 | 1.40 | 0.70* |
| 5 | 0.54 | 0.43* | 0.74 | 0.96 | 0.48* |
| 6 | 0.50 | 0.38* | 0.66 | 0.86 | 0.44* |
| 7 | 0.44 | 0.34* | 0.59 | 0.77 | 0.39* |
| 8 | 0.42 | 0.32* | 0.55 | 0.73 | 0.37* |

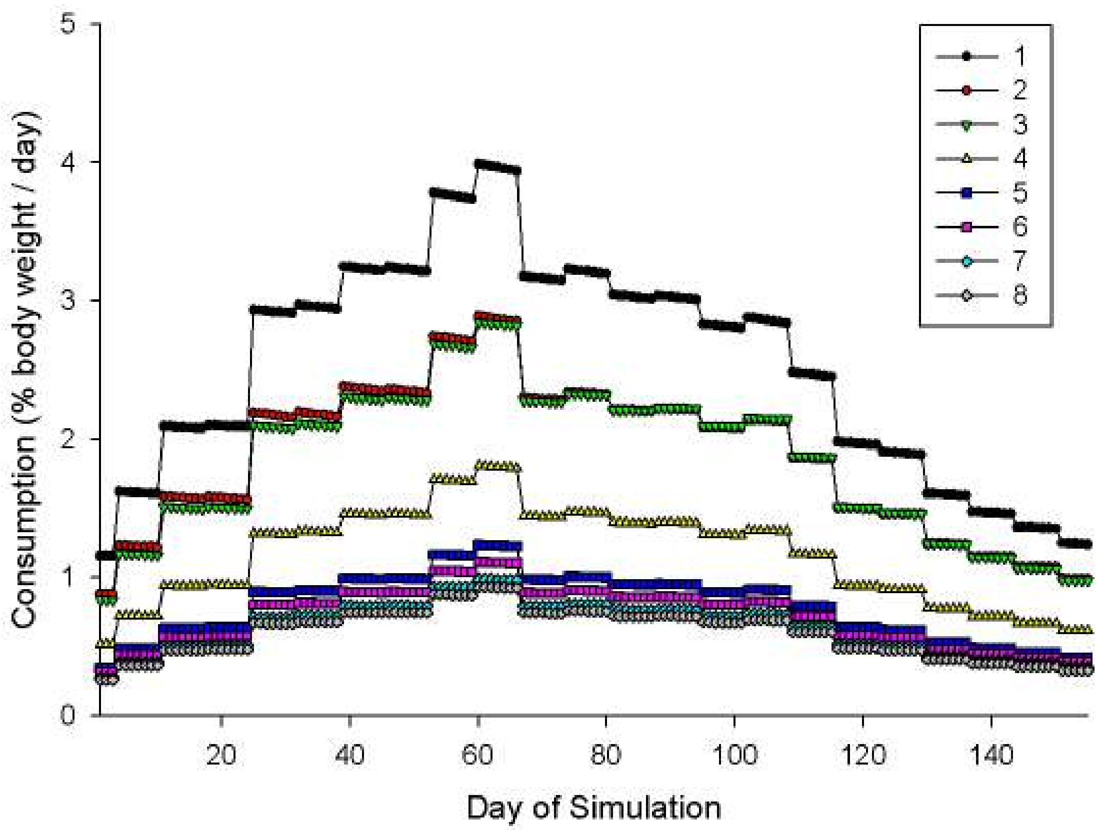


Figure 41. Individual consumption rates (%body weight·day$^{-1}$) of Tahoe Keys bass, cohort's 1 to 8, shown for each day of model simulation. Day 1 of the model was 25 May 06 and day 155 was 26 Oct 06.

*Potential Impacts from Consumption by Bass (Layer 3)*

There was little variability in consumption estimates across all model locations. Individual fish consumption rates scaled to minimum and maximum bass densities yielded a mean (n=50) total consumption by 2 $bass \cdot ha^{-1}$ of 0.89 $kg \cdot 155d^{-1} \pm 0.04$ kg, and by 50 $bass \cdot ha^{-1}$ of 26.04 $kg \cdot 155d^{-1} \pm 0.92$ kg (Figure 42). The difference between maximum and minimum consumption estimates among all nearshore sites was 0.15 $kg \cdot ha^{-1}$ and 3.73 $kg \cdot ha^{-1}$ for 2 and 50 $bass \cdot ha^{-1}$ respectively. For reference, 1 kg of biomass equals approximately 102 native cyprinids, assuming the mean weight of a given native cyprinid is 9.8 g (Thiede 1997). Beauchamp et al. (1991) nearshore fish biomass (NB) was highly variable (Table 23). Mean NB across sites surveyed by was 170.32 $kg \cdot ha^{-1}$ (~17,000 native cyprinid fish) $\pm$ 289.97 $kg \cdot ha^{-1}$ (n=35). Two $bass \cdot ha^{-1}$ would consume $\geq$100 % of nearshore fish biomass at 26 % of nearshore fish biomass sites, and 49 % would be depleted by predation from 50 $bass \cdot ha^{-1}$ (Table 23). Using only the highest NB value at each nearshore site (n=25; Figure 43), proportion of nearshore biomass consumed by bass, $P_{NB}$, was $\geq$100 % of nearshore biomass at 12 % and 36 % of nearshore sites for 2 $bass \cdot ha^{-1}$ and 50 $bass \cdot ha^{-1}$ respectively (Figure 44).

Contemporary data of nearshore fish biomass could elucidate where prey densities might elicit movements to non-vegetated habitats. Furthermore, comparing nearshore biomass estimates to total bass consumption could identify where native littoral fishes are at risk of being depleted. Without contemporary estimates we found, based on historical data, that bass would have the greatest impact to littoral fish populations on the west shore north of Meeks Bay, at one site within Crystal Bay, and one site on the southwest shore above Zephyr Cove (Figure 44). This assumes that there is no density-dependence response from the natives while they are being predated (i.e. once a fish is eaten, that biomass is not replaced until next summer). Also it is important to note that interpretations are limited by geographic extent; there are no nearshore biomass estimates in the south shore where bass presence is concentrated.

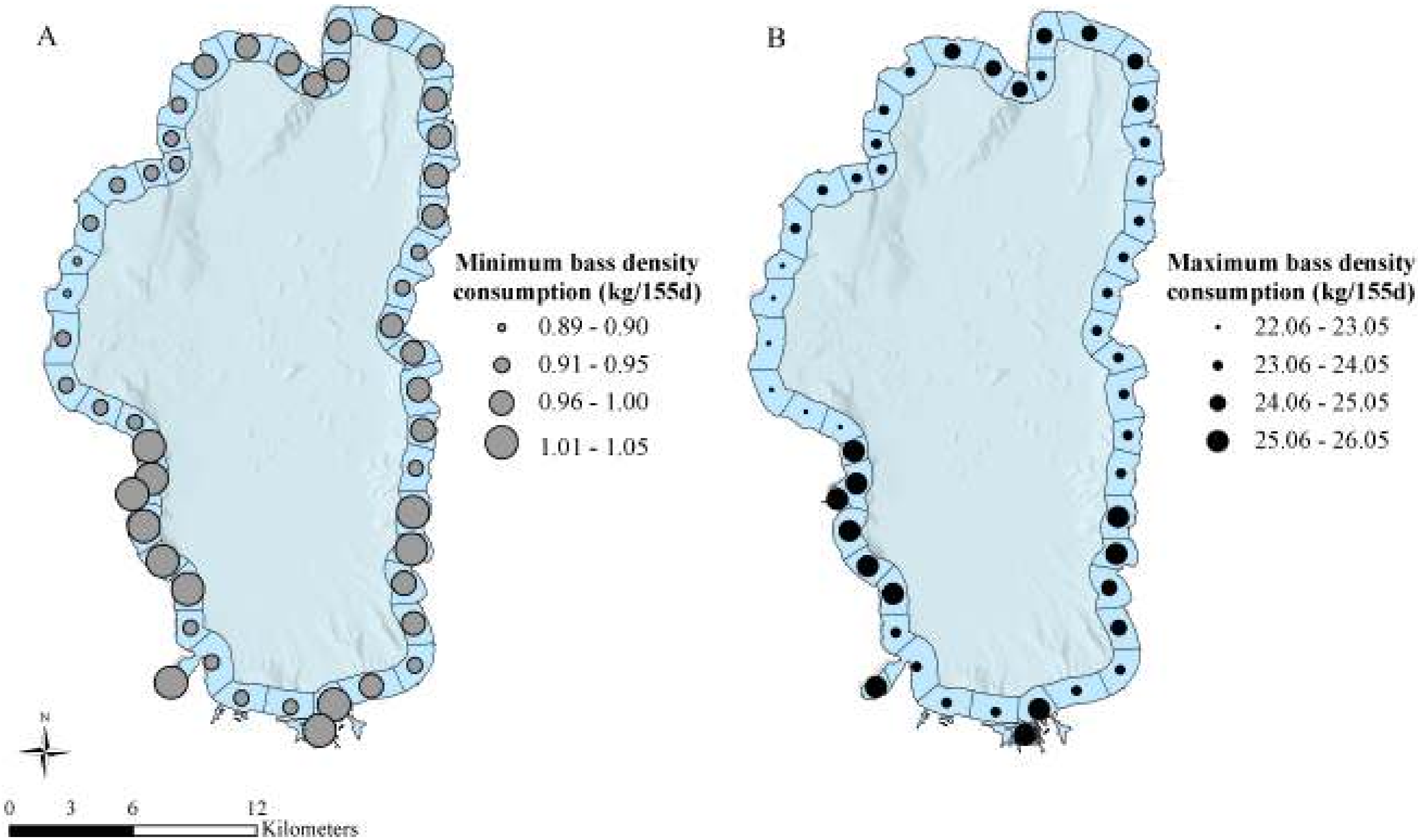


Figure 42. Total bass consumption during the model period ($kg \cdot 155\ d^{-1}$) by (A) minimum ($2\ bass \cdot ha^{-1}$) and (B) maximum ($50\ bass \cdot ha^{-1}$) bass densities. Bass densities were observed from snorkel surveys at 20 sites (Tahoe Keys mean density = $34\ bass \cdot ha^{-1}$). Note the intervals for symbol sizes differ between (A) and (B).

Table 23. Proportion of nearshore fish biomass ($P_{NB}$) consumed by 2 and 50 bass·$ha^{-1}$ at all 35 sites observed by Beauchamp et al. (1991). The nearshore sites coincident with Beauchamp et al. (1991) sites are listed. *Denotes the highest nearshore biomass (NB) observed per nearshore site. Sites are listed in clockwise order from North Stateline (KB) just west of Crystal Bay.

| **Nearshore Site** | **Biomass Site Code** | **Biomass Site Name** | **Nearshore Biomass (NB)** (kg·$ha^{-1}$) | **Percent Biomass Consumed ($P_{NB}$)** 2 bass·$ha^{-1}$ | **Percent Biomass Consumed ($P_{NB}$)** 50 bass·$ha^{-1}$ |
|---|---|---|---|---|---|
| 0 | KB | Kings Beach | 16.80 | 5.8 | >100 |
| 4* | CRYSCOND | Crystal Bay Condominiums | 82.47 | 1.2 | 29.9 |
| 4 | HULLAR | Hullar Estate | 0.03 | >100 | >100 |
| 4 | INCLINE | Incline Village | 6.9 | 14.3 | >100 |
| 5 | HIDECK | Hidden Creek | 22.26 | 4.5 | >100 |
| 5* | STUNNCK | S. Tunnel Creek | 329.97 | 0.3 | 7.6 |
| 6 | SANDH | Sand Harbor | 244.27 | 0.4 | 10.1 |
| 7* | SANDPT | Sand Point | 0.19 | >100 | >100 |
| 7 | SANDPTB | Sand Point B | 0 | >100 | >100 |
| 8 | NWHITT | N. Whittel's mansion | 7.17 | 13.3 | >100 |
| 8 | WHITTELS | Whittel's mansion | 82.23 | 1.2 | 29.1 |
| 8* | CHIMB | Chimney Beach | 317.4 | 0.3 | 7.5 |
| 9 | ANVILRK | Anvil Rock | 371.3 | 0.3 | 6.4 |
| 12 | DEADM | Deadman's point | 57.15 | 1.7 | 41.6 |
| 15 | LOGANSH | Logan Shoals | 0 | n/a | n/a |
| 16 | NCAVERO | N. Cave Rock | 2.58 | 36.8 | >100 |
| 16* | CAVER | Cave Rock | 8.01 | 11.9 | >100 |
| 20 | STATEL | South Stateline | 1285.78 | 0.1 | 1.9 |
| 29 | DLBLISS | D.L. Bliss State Park | 751.25 | 0.1 | 3.4 |
| 30 | RUBICON | Rubicon Point | 756.11 | 0.1 | 3.4 |
| 33 | SUGARPT | Sugar Pine Point | 0.74 | >100 | >100 |
| 34* | SUGARPR | Sugar Pine Pier | 13.02 | 7.7 | >100 |
| 34 | NSUGAR | N. Sugar Pine Point | 0.08 | >100 | >100 |
| 35 | CHAMLD | Chamber's Landing | 6.12 | 14.9 | >100 |
| 36 | NCHAMB | N. Chamber's Landing | 7.2 | 12.7 | >100 |
| 37* | HOMEWD | Homewood | 172.11 | 0.5 | 13.2 |
| 37 | NHOMEWD | N. Homewood | 0.05 | >100 | >100 |
| 38* | FLUER | Fluer de Lac | 40.62 | 2.2 | 55.7 |
| 38 | KASPIAN | Kaspian Point | 0.04 | >100 | >100 |
| 39 | WARDCK | Ward Creek | 184.8 | 0.5 | 12.1 |
| 40 | SUNNY | Sunnyside | 0.26 | >100 | >100 |
| 41 & 42 | BOATW | Boatworks Marina | 690 | 0.1 | 3.4 |
| 44 | DOLLAR | Dollar Point | 28.24 | 3.3 | 82.9 |
| 45 | CHINQ | Chinquapin | 283.13 | 0.3 | 8.4 |
| 48 | TAHOEVIS | Tahoe Vista | 192.93 | 0.5 | 12.5 |

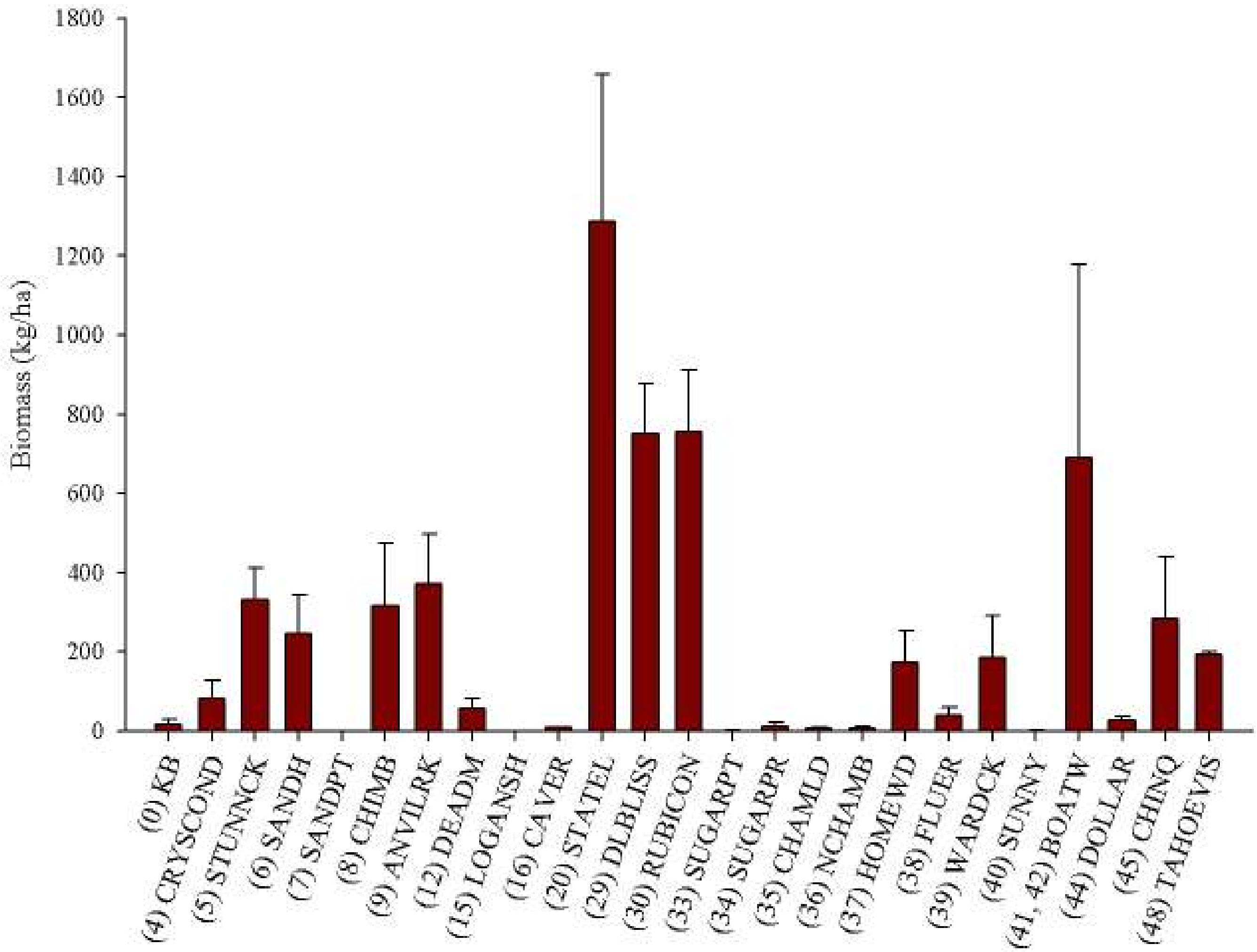


Figure 43. Beachamp et al.'s (1991) highest nearshore fish biomass (NB) observed per nearshore site, which is noted in parentheses. Biomass at 1, 3, and 10 m were divided by transect area (0.04 ha) then summed to calculate biomass density ($kg \cdot ha^{-1}$). If a nearshore biomass survey occurred multiple times at the same site within April to September, biomass was averaged for each depth and then summed, so that nearshore biomass was not inflated. Total NB represented prey biomass available to bass during summer months. Sites are listed in clockwise order from North Stateline (KB) just west of Crystal Bay. See "Table 23" for full site name.

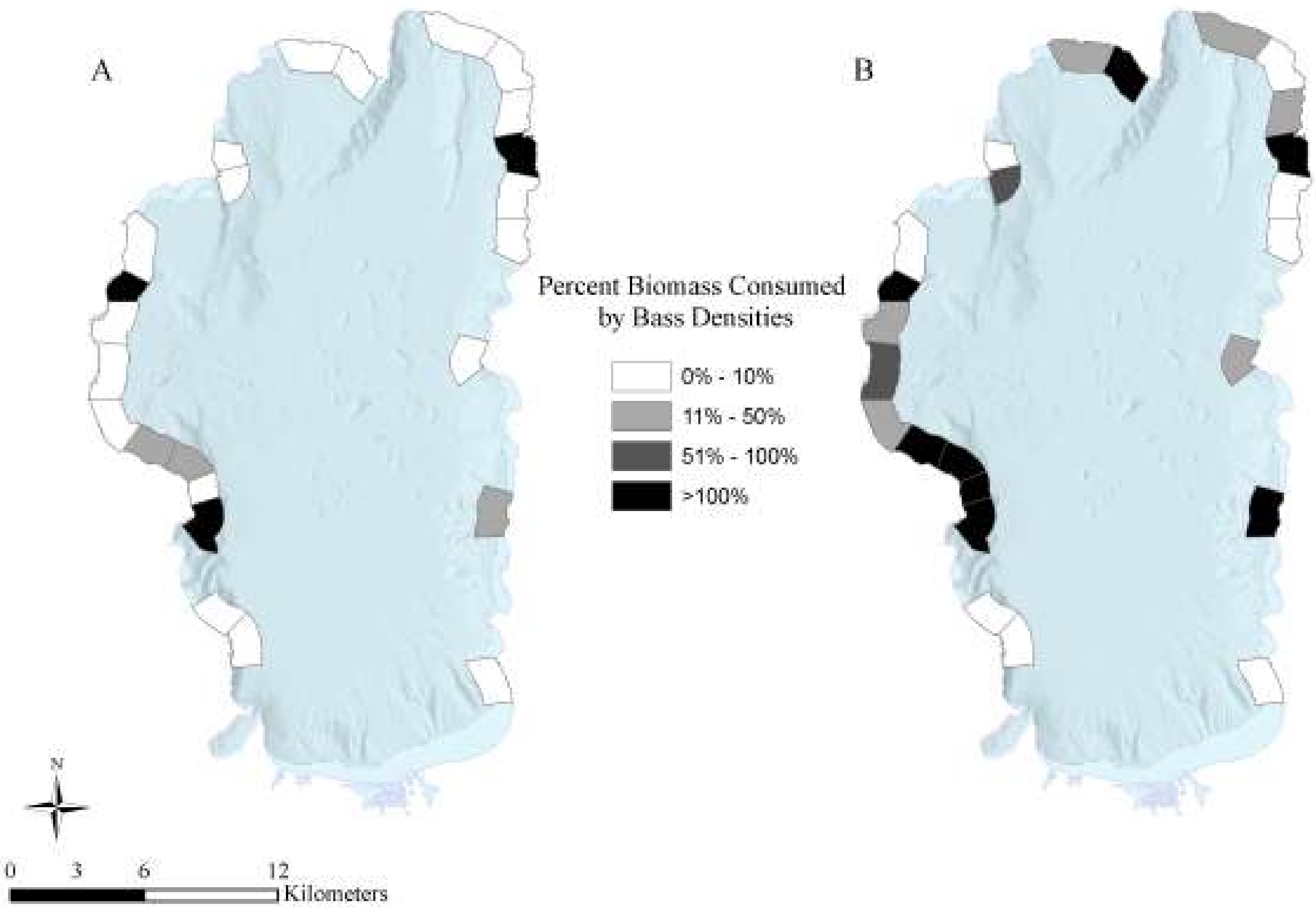


Figure 44. Percent of nearshore fish biomass ($P_{NB}$) potentially consumed by minimum and maximum bass densities observed in Lake Tahoe in 2006. The highest native biomass value from Beachamp et al. (1991) was compared to bass consumption at each site shown. (A) 2 bass$\cdot$ha$^{-1}$would consume $\geq$100 % of biomass at 12 % of sites; (B) 50 bass$\cdot$ha$^{-1}$ would consume $\geq$100 % of biomass at 36 % of sites.

Although sites with the greatest perceived impact to native fishes are based on historical data, consumption rates of current and hypothetical bass alone anticipate the range and magnitude of predation expected throughout the nearshore. Consumption rates, driven by nearshore temperatures, were relatively equal across sites with slightly elevated rates in the warmer northeast and southern sites. Assuming the average native cyprinid weighs 9.8 g (Thiede 1997), two bass$\cdot$ha$^{-1}$ would eat 15 additional native fish (0.15 kg$\cdot$155 days$^{-1}$) during the growing season at the site with the highest observed consumption rate compared to the lowest site, and 50 bass$\cdot$ha$^{-1}$would consume an additional 380 fish (3.75 kg$\cdot$155 days$^{-1}$). In addition, mean native fish abundance is patchy and highly variable (Beauchamp et al. 1994), thus consumption estimates with limited intra-site variability do not highlight sites of elevated conservation concern relative to others.

Regardless, consumption estimates and bass diet data indicate that bass predate native fish where they occur and will likely endanger native fishes as they proliferate nearshore. Theide (1997) observed that predation from pelagic-based lake trout led to native littoral fish declines, suggesting that further declines are likely as bass are nearshore predators whose habitats directly overlap native littoral fishes. Managers can anticipate the level of predation that can occur, given our bass consumption estimates, but should know that consumption levels are based on diets from Tahoe Keys bass alone, and this study does not address how consumption rates vary with diet composition. Without diet data from locations outside the Tahoe Keys, it was necessary to assume that Tahoe Keys bass diets represented diets at all other sites. As a result consumption at non-Tahoe Keys sites may be underestimated because native forage fish abundance is lower in Tahoe Keys compared to many other sites modeled (Beauchamp et al. 1994; Reuter and Miller 2000; Kamerath et al. 2008).

Tahoe Keys consumption estimates suggest that consumption by bass in Lake Tahoe is lower than other mid-latitude lakes. In Lake Rebecca, Minnesota mean bass consumption estimates from bioenergetics models were 63 % higher than Tahoe Keys mean consumption for bass cohorts 1 to 8 (Cochran and Adelman 1982). Additionally, field measurements of maximum consumption by bass in Lake Rebecca were ~3 times higher than the observed maximum in the Tahoe Keys (Rice and Cochran 1984). Lower consumption rates could partially be due to the exclusion of spawning losses from this study's model, or warmer thermal regimes within the Tahoe Keys. A proportionality constant, P, was calculated independent of the Wisconsin model estimate for this study using values from Niimi and Beamish (1974) for a 150 g (cohort 3) bass at temperatures resembling the Tahoe Keys. The resulting P of 0.59, was in close corroboration with the Wisconsin model estimate, P = 0.57.

Wisconsin model estimates are subject to the usual sources of error including: uncertainty in the activity multiplier, sensitivity in prey energy densities, and using mean proportion of diet items rather than medians (Cochran and Adelman 1982; Beauchamp et al. 1989; Ney et al. 1993). Additionally, energy lost to spawning was unaccounted for in our model, which would additionally underestimate consumption rates for Lake Tahoe. However, if Tahoe Keys consumption rates approximate *in situ* consumption, and Lake Tahoe consumption is indeed lower than other lakes, we would expect bass growth in Lake Tahoe to also exhibit lower growth compared to other systems. Comparing Lake Tahoe bass to the national standard revealed that Tahoe Keys bass growth rates are, on average, 68 % below the North American standard developed by Jackson et al. (2008). This is a not an unexpected result for a warmwater fish inhabiting a mid-latitude, oligotrophic lake at high elevation. Cohorts two through eight approached the 5$^{th}$ percentile, and cohort one approached the 10$^{th}$ percentile of mean lengths at ages calculated from North American populations (Jackson et al. 2008). Cohort one lengths could be higher as a result of ageing error, or selection could be stronger for rapid growth in young-of-year to avoid over-winter mortality (Garvey et al. 2004). Tahoe Keys bass condition factors were lower in May 2007 compared to August 2006 for cohorts one through four, suggesting over-winter mortality from starvation occurs, and may be limiting bass establishment (Post et al. 1998). A warming climate will decrease winter duration, and the potential effectiveness of over-winter mortality as a limiting factor for bass establishment (Shuter et al. 1980).

Climate change is shifting Lake Tahoe thermal regimes closer to optimum temperatures and increasing habitat suitability, making bass establishment a long-term management issue (Ngai 2008). As thermal constraints relax, bass growth and consumption would likely increase unless limited by food-availability (Hill and Magnuson 1990; De Stasio et al. 1996; Petersen and Kitchell 2001). Considering that predation is a common cause of cyprinid mortality, and nearshore fish abundance could be further depressed and perhaps eliminated by bass, which would deplete a bass' fish prey base (Lyons and Magnuson 1987; Thiede 1997). However, bass may not be limited by depletion of fish prey base; Lake Tahoe contains an underutilized introduced crayfish (*Pacificus lenticulatus*) in high nearshore densities (Flint and Goldman 1975). Crayfish are common in bass diets (Heidinger 1975), and have no native predator in Lake

Tahoe. Thus, crayfish are poised to buffer food-limitations for bass, similar to mysid shrimp subsidization of lake trout diets (Chandra et al. 2005). The crayfish subsidy could allow continued growth despite greater consumptive demands in lieu of increasing lake temperatures. Climate induced increases in bass consumption rates will exacerbate predation pressure on Lake Tahoe's native cyprinids, as has been true of other non-native warm water piscivores in the Columbia River (Petersen and Kitchell 2001), and increase consumption of crayfish which could recycle additional nutrients nearshore.

**Conclusions and recommendations**

Our current assessment of warmwater fish distribution indicated the densities of these fish are still very low compared to other ecosystems and can be variable over time. Over all the densities were low around most of the lake with higher densities in some locations such as Meek's Marina and intermediate densities in the Tahoe Keys. Anecdotal observations indicated that bass may be in open water areas of the lake, however it is unclear the extent fish have established in these areas or if they were migration zones before they reach more enclosed sites such as marinas and embayments.

The ability of warmwater fishes to grow, reach maturity and spawn, and compete and/ or prey on native fishes and nonnative crayfish is largely governed by thermal regimes, thus information gathered from temperature data around the lake can lend to determining which location will have the most likely area of invasion. Our temperature models, both coarse enclosed versus nonenclosed site analysis via cluster analysis, and fine scale models developed from MODIS satellite information showed that all neashore locations (monitored and otherwise) were thermally suitable for invasion of largemouth bass, bluegill, and likely other warm-water fishes. The finer scale, two km resolution model developed for bass was unique because it predicts establishment likelihood of non-native bass in an early invasion stage at an intra-lake scale. Vegetation assigned at this resolution indicated that largemouth bass likely utilize vegetation and will establish in nearshore areas containing nonnative water milfoil. In order to prevent the widespread bass establishment in Lake Tahoe and determine future impacts over time we recommend 1) establishing a monitoring program for the nearshore fish community, 2) continue a quantitative evaluation of the Tahoe Keys which is likely a source population of warmwater fishes for other parts of the lake, and 3) initiate a program to manage warmwater fish and invasive plants that contribute habitat for these fish in the Tahoe Keys and other locations, and 4) conduct research on other resource controls (crayfish and ultraviolet light) that may contribute to the regulation of fish communities.

**Monitoring.** The monitoring should at minimum monitor sites classified as highly likely for bass establishment, including misclassified sites as suggest by other models (see MacIssac et al. 2000; Vander Zanden et al. 2004), any habitats containing aquatic vegetation including areas of future expansion, and sites with bass present as these are areas likely to contain bass in the future. If conserving native species is a top priority, nearshore areas known to promote spawning and rearing of native fishes should be monitored. Unfortunately the model we developed to predict impact to native fishes utilized information collected in the early 1990's. Thus, a contemporary assessment of native fish densities in the nearshore is crucial to refine areas that should be monitored and managed in the future. Monitoring for bass could effectively be completed by snorkel surveys within the littoral zone of the areas suggested by this study. Snorkeling would not require diving and should take place 3-4 times in the year during the warmest months. All sites should be monitored monthly starting before temperatures are suitable for spawning and through the growing season. This will ensure that the fishes are captured during spawning and potentially as they move from one location to another.

**Tahoe Keys monitoring and management.** Our movement study indicated that warmwater fish move out of the Tahoe Keys during summer and late fall periods suggesting that the Tahoe Keys may be an important source population for the rest of the lake. Peak temperatures occurred in late July. As climate change progresses, this date is expected to recede earlier in the season and potentially increase the growing season for warmwater fishes. Thus, we recommend continued, quantitative monitoring of the Tahoe Keys populations and a program to manage their numbers and habitat (e.g. invasive plants). Minimal monitoring includes sampling fishes at the beginning, middle, and end of the summer growing season and measuring basic ecological traits such as population size structure, catch, diet, and body condition as well as the presence of native fishes. Based on the age classes of the bluegill and bass species, continued management on regular two- to three-year intervals after an initial two consecutive years of management can control existing populations and prevent further establishment. This should reduce piscivory upon and competition with native fishes while reducing non-native population size. Long-term management is critical because the increasing popularity of these nonnative fishes with anglers which was not observed when the first warmwater fish evaluations were made in 1999 and 2003 (Chandra and Allen, unpublished data). Since the densities of warmwater fishes are currently fairly low compared to other lake ecosystems, we recommend implementing a control and management program in other part of the lake where fishes have been observed. This can be accomplished with multiple methods during a field season including electroshocking, gillnetting, and angling.

**Future research for more accurate predictions of warmwater fish establishment.**

The models developed here are derived from primary factors (temperature and habitat) that contribute to bass growth and reproduction. In order to refine the bass models and more precisely predict the locations of other warmwater fishes (bluegill) impacts to native fish biodiversity, we recommend that 1) models use existing temperature data and diet information to create models for bluegill, the dominant warmwater fish shown in this study to compete with native fishes and other potential invaders such as smallmouth bass that will likely have a greater impact on native fishes, and 2) include other factors into the existing bass model such as food resource controls on bass distribution and energetics as well ultraviolet light impacts on larval recruitment. Crayfish are a preferred food sources for bass in their native habitats. Currently the invasive crayfish in Lake Tahoe seem to have expanded in population since estimates were first made in the 1970's with over 230 million individuals in the lake estimated in 2001 (Chandra unpublished data). The bioenergetics model created for this study does not account for this resource in the lake and how they may contribute to bass growth and maintenance. Furthermore, research by our colleagues at the Miami University in Ohio (Williamson, Oris, and Tucker unpublished) using Lake Tahoe fishes indicates that ultraviolet light penetration may be controlling recruitment of nonnative fishes and allowing the persistence of native fishes. Thus, there may be direct ties between the lake's clarity and the distribution of warmwater fishes. These two resource controls of food availability and physical light constrains should be incorporated into the existing model to refine areas for monitoring as well as management.

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