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Abstract

In watersheds with diverse instream habitats, such as the Betsie River in northern Michigan, production of early life history stages of fishes can be concentrated into a few critical habitat units. The Betsie River watershed is atypical of the neighboring watersheds due to its thermal properties. The main channel supports a popular migratory salmon and steelhead fishery, but is marginal habitat for resident trout because summer temperatures are high. Tributaries in the watershed are spring-fed and provide colder habitats in summer. The objectives of our study were to quantify the density and mortality of steelhead *Oncorhynchus mykiss* parr throughout the watershed and to evaluate the influence of different thermal macrohabitats on steelhead parr production. From 1993-1996, parr abundance was estimated at 14 sites by use of depletion sampling and smolt out-migration was estimated by visual methods. Density of steelhead parr ranged from 0/ha to 3000/ha at sampling sites. We found 62% of age-0 parr and 50% of the age-1 parr in the main channel. The remaining parr were found in the tributaries which comprise only 11% of the total stream area in the watershed. Smolts out-migrated at annual densities ranging from 11.9/ha to 22.0/ha. Annual instantaneous mortality rates (Z) ranged from 0.710 to 3.578 and were the greatest for age-1 and age-2 parr. Mortality was greater during severe winters and at sites in the main channel. Because many parr were found in the few tributaries sampled, and because survival was higher in these streams, the small tributaries are valuable to the overall production of steelhead from this watershed.

Introduction

Steelhead *(Oncorhynchus mykiss)* were introduced into the Great Lakes Basin in 1867 and since their introduction, naturalized populations have become established in many Great Lakes tributaries (Latta 1974, Biette et al. 1981). Great Lakes steelhead migrate into streams in both the winter and spring and spawn in the spring. Juveniles typically spend 1-3 years resident in the tributary watershed before migrating to the lake, where they grow for 1-3 years before reaching sexual maturity (Biette et al. 1981, Seelbach 1993). In most streams, the majority of juvenile steelhead spend 2 years in the river while fewer spend only 1 or 3 years in the watershed (Biette et al. 1981).

Water temperature can limit a population of salmonids by high summer temperatures or low winter temperatures that exceed the tolerance limits (0 - 25°C; Wismer and Christie 1987). Effects of temperature may include mortality, metabolic challenges and decreased growth (Adams and Breck 1990), or fish may distribute themselves throughout the watershed in the most preferred thermal areas (Nielson et al. 1994, Peterson and Rabeni 1996), leading to competition for space or a carrying capacity that is a function of thermal availability. Many of the southern streams in Michigan are marginal for resident trout due to high summer temperatures, yet returns of both wild and hatchery steelhead to these rivers can be very large (Seelbach 1989). Currently, little information exists on the numbers of juvenile steelhead that can be produced or their population dynamics in watersheds dominated by marginal thermal habitat (Seelbach 1989, 1993).

Severe winters can be detrimental to a cohort of steelhead with mortality of 50-90% reported in some studies (Maciolek and Needham 1951, Seelbach 1987). Partial explanation for the mechanisms behind winter mortality may be limiting microhabitat. In water below 8°C, salmonids are known to reduce activity and seek cover (Campbell and Neuner 1983). Preferred winter habitat for steelhead parr includes groundwater fed side-channels, complex woody debris, the interstitial spaces within boulders or rubble along stream margins, under cobble, and in water less than 30 cm deep with near-0 water velocities (Everest and Sedell 1983, Campbell and Neuner 1984, Heifetz et al. 1986, Swales et al. 1986). In northern streams, low temperature conditions can exist for months at a time and in predominantly sandy substrate streams, overwintering habitat may be critically limiting (Bustard and Narver 1975, Swales et al. 1986).

Many stream rehabilitation or restoration projects focus on the improvement of instream habitat and reduction of erosion throughout the watershed. Knowledge of the critical production areas for wild steelhead in streams can help to prioritize and implement important watershed management activities such as protection of riparian vegetation, a reduction in erosion, and the addition or manipulation of instream habitat.

The objectives of this study were to:

1) describe steelhead parr population dynamics in a watershed with marginal habitat for salmonids

2) quantify and compare the spatial and temporal distribution of steelhead parr throughout the watershed

3) estimate total production of juveniles in the watershed, and

4) evaluate mortality rates and their relationship with thermal conditions in the watershed.

Study Site

The Betsie River watershed is located in northwestern corner of the lower peninsula in Michigan (Figure 1). The watershed is one of the smaller watersheds in Michigan tributary to Lake Michigan (67,126 ha). The river begins via an unregulated, natural surface outflow from Green Lake and flows for approximately 79 km before reaching Betsie Lake, which flows into Lake Michigan at Frankfort (44°W, 86°N). The gradient is low (0.002%) and the river flows through a landscape dominated by glacial moraines. Land use in the watershed is predominantly light agriculture and timber production and very little urban development exists. Several small tributaries drain into the Betsie River. The Little Betsie River and Dair Creek are the two largest with mean flows of 0.51 and 0.44 m^3/s. Small spring-fed tributaries that are approximately 1.0 m wide and 5-30 cm deep are prevalent throughout the watershed. The river has no permanent discharge gages, but summer flows measured through the course of the study ranged from 4.0 to 12.7 m^3/s with a mean flow of 5.5 m^3/s.

Fish surveys have shown a predominance of white suckers *Catostomus commersoni*, hornyhead chubs *Nocomis biguttatus*, creek chubs *Semotilus atromaculatus*, and blacknose dace *Rhinichthys atratulus* (Wicklund and Dean 1958, MDNR, Fisheries Division Stream Surveys, 1990), yet the Betsie River supports popular steelhead, chinook *Oncorhynchus tshawytscha* and coho salmon *Oncorhynchus kisutch* sport fisheries. The steelhead fishery is supplemented by stocking of hatchery fish in the river, but no coho or chinook salmon are stocked.

Recent changes in the watershed have increased interest in the potential production of wild steelhead. Thompsonville Dam, which was located in the mid-reaches of the watershed (Figure 1) failed in the spring of 1989. Downstream sedimentation and streambank erosion is still evident from this event. However, the upper 14.9 km of the watershed is now available for the production of migratory salmonids including steelhead.

Methods

We stratified sections of the river channel according to differences in temperature regimes, discharge, and gradient, resulting in the following designations: upper Betsie River (sites 1-4), lower Betsie River (sites 5-8), large tributaries (sites 9-10, and 13-14), and small tributaries (sites 11-12)(Figure 1). All 14 sites were sampled in the same two weeks in late July (1993-1996) and mid-October (1994-1995) to determine steelhead parr abundance. We used a 250 volt DC electrofishing barge unit and multiple pass depletion methods to capture parr (Zippen 1958). Block nets were placed at the upstream and downstream margins of the sites prior to electrofishing to address the removal-estimation assumption of a closed sampling site. At the time of capture, we anaesthetized steelhead parr with MS-222, and then measured total length (mm) and weight (g), and removed scale samples from an area above the lateral line, below and posterior of the dorsal fin origin (Jearld 1983). Fish were checked for fin clips to identify their origin (hatchery or wild) and were released downstream of the sample site. Age structure of the population was determined through length-frequency analyses and scale pattern analysis. Scales were also inspected to determine whether the fish had been produced in a hatchery and then remained in the river after stocking (Seelbach and Whelen 1987).

Maximum likelihood estimates of abundance and confidence intervals were calculated for each site from the removal data by use of Microfish 3.0 (Van Deventer and Platts 1983, 1985, 1986). Because of small estimates for steelhead parr at many sites, a total steelhead site estimate was calculated and proportions of each age-class captured were multiplied by the overall estimate to get an age-class estimate according to

$$n_{ac} = P_{ac} * M \qquad \text{(Equation 1)}$$

and,

$$\mathrm{Var}\ (n_{ac}) = P_{ac}{}^{2} * \mathrm{Var}\ (M) \qquad \text{(Equation 2)}$$

where n_{ac} = the number in each age class, P_{ac} = the proportion captured in each age-class, and M = the estimate of the total number of steelhead parr in the site. Density per hectare by age-class was calculated by

$$d_i = n_i / a_i, \text{ and } \mathrm{Var}\ (d_i) = 1/a_i^2\ \theta^2_I \qquad \text{(Equations 3 and 4)}$$

where d_i = the age-specific density at site i, a_i = the area in hectares at site i, θ^2_i = the variance for the estimate at site I. Mean densities for the Betsie River, Little Betsie River, Dair Creek, and the two small tributaries were calculated by

$$D_{t\,=}\ \Sigma\ d_i / n, \mathrm{Var}\ (D_t) = 1/n^2 \qquad \text{(Equation 5 and 6)}$$

where D_t = the density for reach or tributary t and n = the number of sites sampled within reach or tributary t. Extrapolations for reach or tributary (Z) abundance of parr were calculated by

$$Z_t = a_t * D_t \qquad \text{(Equation 7)}$$

and,

$$\text{Var}\ (Z) = A^2 * (\text{Var}\ D_t) \qquad \text{(Equation 8)}$$

where Z_t = reach or tributary abundance and a_t= area in the reach or tributary t. And finally, the overall watershed estimate of abundance (N) was calculated for each age-class by

$$N = \Sigma Z_t \qquad \text{(Equation 9)}$$

and,

$$\text{Var}\ (N) = \Sigma\ \text{Var}\ Z_t \qquad \text{(Equation 10)}$$

where N = total watershed abundance for age-class.

Mean length of each age class was analyzed for differences between sample reaches by use of general linear models (SAS). We evaluated summer and fall data separately.

Estimates of the number of outmigrating steelhead smolts were determined each May-June, 1993-1996, by use of a visual method (Newcomb and Coon 1997). In addition to estimating total abundance of smolts, we determined the species composition and origin (hatchery/wild) of the smolts by use of traps every fifth day in the smolting period (Newcomb and Coon 1997).

Instantaneous mortality rates were calculated according to Ricker (1975) for sample reaches and the watershed. Estimates of interest included mean annual mortality and within year rates for winter (October-July) and summer (July-October). We assumed that by October, the parr population had experienced the full effects of summer conditions and the population represented pre-winter abundance. We also assumed that by July, all age-0 steelhead were large enough to be captured by electrofishing gear and that all emigrating fish had left the watershed.

Temperature was monitored at 7 sites in the watershed that corresponded to electrofishing sites. We recorded temperature hourly by use of Stowaway™ (Onset Instruments) recording devices. The Stowaways™ were tested in a water bath using an ASTM thermometer to check the accuracy and to assess the need for calibration adjustments. Stowaways™ were located in the channel where the water was continuously flowing, out of direct sun, and approximately 3 cm above the substrate. We calculated daily, weekly, and monthly means from the hourly records. Missing data points were filled in with regression analysis from upstream and downstream locations. For each year, we calculated mean summer (June, July, and August) and winter (December, January, and February) temperature and determined maximum and minimum temperatures for each monitoring location. In addition, we obtained air temperature data from the weather station in Cadillac (NCDC) and calculated winter severity as a function of number of days with a mean daily temperature less than -12°C (Seelbach 1987).

Results

Reach Characteristics

The channel morphometry, discharge, and thermal characteristics varied widely among the sample reaches (Table 1). Discharge doubled between the upper and lower reaches of the Betsie River with only a 2.7 m increase in mean channel width and a 0.1 m increase in mean channel depth. Mean summer discharge varied annually. In 1995, very little snow melt and lack of spring rain resulted in low flow conditions. In 1993 and 1996 the opposite occurred with large snow melt flows followed by high volumes of spring rain and higher summer flows for both years (Figure 2).

Water Temperature and Environmental Variability

Water temperature regimes varied spatially and temporally throughout the watershed. Winters of 1993-1994 and 1995-1996 were unusually cold, with over 20 days of mean daily air temperature less than -12°C (Seelbach 1987, Tables 2 and 3). Summer, 1995 was a drought year and the mean air and water temperatures were the highest recorded in four years of study (Tables 2 and 3).

Mean and maximum summer temperatures from stations throughout the watershed were as much as 6 to 8°C different on any given day. The upper Betsie River exhibited the greatest extremes in temperature with the warmest summer (>25°C) and coldest winter temperatures (< 0°C). The lower Betsie River reaches were not as extreme, but exhibited a wider range of temperatures than the tributaries, Dair Creek and Little Betsie River (Table 4). Dair Creek was the tributary most dominated by groundwater and was typically the coolest in the summer and the warmest in the winter. The Little Betsie River was similar, but usually slightly warmer in the summer and cooler in winter (Table 4).

Number of Outmigrating Smolts

In May and June (1993-1996), we captured a total of 1,775 steelhead smolts by electrofishing. Scale samples were collected from a subsample (727 smolts) to determine age and origin, and then all hatchery fish were excluded from further analyses. The mean length of wild smolts ranged from 188 to 191 mm and the age-structure of the yearly emigration was comprised of 48-54% age-1 fish, 40-46% age-2 smolts and 0-10% age-3 smolts. The spring of 1996 was different in that over 78% of the smolts captured were age-1 and only 20% were age-2. Less than 3% of the smolts in 1996 were age-3. Fewer than 3,000 wild steelhead smolts left the watershed each year (Table 5). The Betsie River produced smolts at watershed densities ranging from 11.9/ha in 1996 to 22.2/ha in 1993 with a mean of 17.5 smolts/ha.

Abundance and Distribution of Parr Throughout the Watershed

From 1993 through 1996, we captured 4,130 steelhead parr in summer and autumn electrofishing. Length-frequency and scale analyses (699 scale samples) from electrofishing in July and October confirmed the predominance of two age classes

(Figures 3 and 4). Age- 0 parr comprised a mean of 63% of the catch, age-1 parr made up 36% and fewer than 1% were age-2 parr.

Density estimates of parr per hectare varied widely throughout the watershed. Values of 0 - 20 parr/ha were common in the upper Betsie River, sites 1-4. The lower sites in the Betsie River (5-8) yielded higher densities, ranging from 0 to 1677 parr/ha (Table 6). The greatest densities of parr were recorded consistently in Little Betsie River, Dair Creek, and the small tributaries, with densities frequently of over 500 parr/ha. Age-2 parr ranged in density from 16/ha to 77/ha when they were present, but we only captured them in the Little Betsie River and Dair Creek in 1994 and 1995.

Reach estimates were calculated from the mean of site abundance to estimate the contributions of each specific reach to the watershed production of steelhead parr. We calculated reach abundance of steelhead parr for the Betsie River, Dair Creek, Little Betsie River, and the small tributaries. The Betsie River reach was further divided into an upper and lower reach for comparison. Density estimates for age-0 parr in Dair Creek, Little Betsie River, and the small tributaries were 2.5 to 18 times greater than the densities observed in the Betsie River (Figure 5). Estimates of age-1 parr densities for the tributary reaches ranged from 2.6 to 18 times their density in the Betsie River. The small tributaries were the exception in 1993 and 1994, when no age-1 parr were found.

Within the Betsie River, the upper and lower reaches also differed in parr density estimates. In all years, densities for both age-0 and age-1 parr were greater in the lower reach. In July, 1994 and 1996, very few parr were found in the upper reaches of the watershed and fewer parr were estimated in the lower reaches (Figure 6). A similar trend occurred in the October sampling. However, more parr were observed in the upper reach in October than in July (Table 7).

Although densities of parr were highest in the tributaries (Figure 5), when the estimates are extrapolated by area to account for total watershed production, the main channel Betsie River produces more age-0 steelhead (Figure 7). Using channel areas of 84.0 ha for the Betsie River, 5.9 ha for the Little Betsie River, and 4.5 ha for Dair Creek, the estimates of age-0 abundance for the Betsie River main channel range from 1,171 to 11,812 age-0 parr while the abundance in the Little Betsie River, Dair Creek and the small tributaries ranged from 314 (± 41.2) to 9739 (± 1462) age-0 parr (figure 7). For age-1 parr, the differences in total abundance between the tributaries and the Betsie River are less and in some cases, a tributary contributed more age-1 parr. In the Betsie River, the total abundance of age-1 parr ranged from 1,232 ± (2,610) to 10,505 (± 3,721). The total abundance estimates in the Little Betsie River and Dair Creek range from 827 (± 124) to 7,080 (± 418 parr). In 1994 and 1995, the Little Betsie abundance of age-1 parr was greater than in the Betsie River. The small tributaries held no age-1 parr in 1993 and 1994 and only a few in 1994 and 1995. When the abundance estimates for all the sampled tributaries were combined, they contributed a mean of 56% of the total for age-0 parr and 67% of the total for age-1 parr, but they comprised only 11% of the total channel area in the study reach (Figure 8).

In terms of watershed production, the overall watershed abundance of each age-class of steelhead parr varied throughout 1993-1996 (Table 8). Age-0 parr increased from 18,795 in 1993 to 32,896 in 1995, but fewer than 10,000 age-0 parr were estimated in 1996. In 1993, the largest abundance of age-1 parr was observed, 18,485, which was more than twice the estimates for 1994-1996. However, the large confidence interval should be noted for 1993. Watershed production estimates for age-2 parr were less than 1,000 fish.

Mortality Rates

Annual instantaneous mortality rates (Z) were calculated for the watershed by including the number of smolts estimated each year from the cohort (Table 9). Annual mortality rates were higher for age 1-2 parr with a mean of 1.943. The mean annual mortality rate for parr age-0 to age-1 was 1.059. Mortality for age 2-3 parr was very large at 2.448.

Parr estimates of mortality were problematic for summer to fall in that more age-1 and age-2 parr were estimated for fall than late summer. This may be attributed to the fact that parr were more widely distributed throughout the watershed in the fall than in the summer. Watershed estimates of mortality from summer to fall were much larger in 1994 and 1995 and were also greater than for age-1 and 2 parr in 1994 (Table 9). In 1995, low flow and high summer temperatures most likely constrained parr to a few areas throughout the watershed and the larger fall estimates were due to larger abundance estimates throughout the entire watershed.

Within year rates of instantaneous winter mortality were calculated from October to July for years 1994-1995 and 1995-1996 (Table 2.9). An adjustment was also added to the summer estimates to reflect cohort survival in the emigrant smolts. Winter mortality rates were greater in 1995-1996 than in 1994-1995 for all age classes.

In addition to total mortality from the watershed level, mortality rates were also calculated individually for the Betsie River, the Little Betsie River, Dair Creek, and he small tributaries (Table 10). We made no adjustment for outmigrating smolts or parr moving between reaches, therefore these rates should be interpreted as loss rates from the reach. Loss rates were the greatest for age-0 parr in the Betsie River and the least in Dair Creek. Loss rates for age-1 parr were high in the Little Betsie River and Dair Creek.

Steelhead Density, Mortality Rates and Temperature Variables

We analyzed several relations between parr density, smolt abundance and mortality rates with discharge and several indices of summer and winter severity. Significant negative correlations were found between the summer densities of age-0 and age-1 parr and the mean and maximum summer temperature (Figures 9 and 10). The correlations were the strongest with age-1 parr and maximum summer temperature.

Significant correlations also were observed with indices of winter severity. Weak relations were observed between the density age-1 parr and the prior winter minimum temperature (Figure 11) and mean winter temperature and the instantaneous mortality rate for reaches throughout the watershed (Figure 12). Using the number of days less than -12°C as a winter severity index, a significant negative relationship (adjusted r^2 = 0.946, p = 0.018) was observed between severe winters and the estimate of outmigrating steelhead smolts (Figure 13).

To evaluate the effects of spring flow during steelhead fry emergence, the summer estimate of age-0 steelhead was examined for a relationship with mean spring discharge in May and June, during steelhead fry emergence. A negative relationship was observed with an adjusted r^2 of 0.771 and $p = 0.079$ (Figure 14).

Observed Differences in Fish Lengths

We used length as an index of growth, and tested for differences in length within a reach through the 4 years and among reaches each year for age-0 and age-1 steelhead parr. Too few age-2 steelhead were sampled to analyze differences in mean length. Because we found significant interaction between year and reach, we analyzed the two factors separately. For age-0 parr, there were no significant differences in within reach mean lengths for the Betsie River, Dair Creek, or the small tributaries from 1993 to 1996 (Table 11). In the Little Betsie River, mean lengths were significantly larger in 1993 and significantly smaller in 1996 than in 1994 and 1995. Between reaches, mean length was significantly larger in the Little Betsie River than the other three reaches. In 1993, mean length in Dair Creek was also significantly larger than in the other reaches.

Age-1 steelhead parr were more variable in their mean length. Within reaches, mean lengths were significantly larger in 1993 and 1995 in the Betsie River and in 1996, mean lengths were significantly larger in the Little Betsie River (Table 11). Between reaches, in 1995, age-0 and age-1 parr in Dair Creek and the small tributaries were smaller than the Betsie River and the Little Betsie River, while in 1996, age-1 parr were significantly larger in the Little Betsie River and significantly smaller in the small tributaries.

By combining site specific temperature data with optimum growth rate information through the four years, differences in rearing conditions may explain some of the observed differences in length (Figure 15). We used a temperature range of 15 - 17°C to define the optimal growth range (Wismer and Christie 1987 and Hokanson et al. 1977), and upper zero growth limit of 23°C and lower zero growth limit close to 0°C. In the upper Betsie River (Sites 1 and 4), steelhead parr spent very little time in the optimal growth zone and more time above the optimum limits, and approaching the zero growth limit. In the lower Betsie River (Sites 7 and 8), the trend was similar, yet parr spent more time during the summer near and slightly above the upper optimum growth limit. In the tributaries (Sites 9 and 14), the difference in thermal regimes had varied results for parr. In these sites, parr spent the most time in their optimum growth zone (> 4 months) and never exceeded the upper growth limit. During the winter months, there were few differences in time spent near 0°C in the lower Betsie River and the tributaries, and slightly more time was spent near the 0°C limit in the upper Betsie River. Little Betsie River was warmer than Dair Creek which may have resulted in the larger mean lengths observed there.

Discussion

Life history characteristics which vary from the norm may indicate that rearing conditions such as extremes in thermal variability are facilitating trends in the population. Over half of the emigrating smolts left the Betsie River watershed at age-1. In most other Michigan streams, the majority of smolts leave at age-2 (Bietee et al. 1981, Seelbach and Miller 1993). Furthermore, although the Betsie River smolts are leaving at a younger age, their mean length (188-190 mm) is typical of the physiological size for steelhead smoltification (Hoar 1988) and also similar to lengths observed for populations in which most fish leave at age-2 (Biette et al. 1981, Seelbach 1993). These population attributes combined with the high rate of homing often observed in steelhead, may indicate that the Betsie River steelhead has the potential to become a discrete stock (Biette et al. 1981). Further study is required to determine if the faster growth observed in parr throughout the watershed is a bioenergetic manifestation or the result of phenotypic selection for faster growth rates in an environment where survival beyond year 1 is highly improbable.

Larger smolts are advantageous to the population and can result in a high rate of return as adults. For example, Ward et al. (1989) found that mean lengths of outmigrating smolts from the Keogh River, age-2 age-3, and age-4 were 153, 177 and 218 mm. However, back-calculation of the returning adults showed that mean lengths for age-2, age-3, and age-4 were 177, 196, and 220 mm. Survival for smolts averaging 140 mm was only 2-3% , but was 37% for 220 mm smolts. Similarly, Seelbach et al. (1994) observed a return rate of 10- 30% for smolts stocked at lengths greater than 200 mm. In the late 1980’s, the Betsie River fishery was found to be over 90% wild fish even though 20,000 steelhead juveniles were stocked in the river each year (Seelbach and Whelan 1988). Betsie River smolts at age-I, 2, and 3 average 170, 188, and 203 mm and it is likely that these larger wild smolts also return at high rates.

Densities of steelhead parr varied widely throughout the Betsie River watershed and can be compared with other studies and tributaries to the Great Lakes (Table 12). The production of parr in the Little Betsie River and Dair Creek is comparable with Sand Creek and Silver Creek located in southern Michigan (Dexter 1993a, 1993b). Interestingly, these streams were also found to have parr with growth rates greater than the average growth found throughout the state. We found far fewer parr in the Betsie River than what was found in the Little Manistee River in northern Michigan and also in the southern Michigan streams.

Incorporation of naturalized production of steelhead in Great Lakes fishery management plans is a fairly recent approach. The basic premise in management of naturalized steelhead populations is that the protection of spawning and rearing habitat can maintain a population and is cheaper and more cost effective than restoration or rehabilitation that often has mixed results (Biette et al. 1981, Peck 1992). Knowledge of the important rearing areas and the limiting mechanisms to juvenile steelhead production throughout the Betsie River watershed can help to prioritize protective and rehabilitative actions to preserve and improve these critical habitat units. By using a watershed approach and incorporating tributaries in estimating parr abundance, we were able to determine the spatial distribution of juvenile steelhead and identify specific reaches of the watershed that were important to overall production. In a watershed similarly limiting by high water temperatures, Roper et al. (1994) also used a basin approach to determine the distribution and abundance of salmonids. They found that abundance estimates based on densities from a limited area in the watershed could have overestimated the juvenile steelhead population by a magnitude of 5 and that significant proportions (25%) of the older juvenile steelhead population were constrained within 12% of the total stream area. While they sampled throughout the entire length of the stream, they did not incorporate tributary streams in their analysis. Similarly in the Betsie River, over 50% of the age-0 and age-1 steelhead parr were found in the tributaries which comprise only 11% of the total channel area.

Tributaries are key to the production of juvenile steelhead in the Betsie River watershed. Not only are the preferred thermal environments provided in the tributaries, but there may also be an advantage to growth. Peterson and Rabeni (1996) observed 2 populations of sunfish in a mainstem river and a tributary and found that the fish that both resided in and seasonally moved into the thermally moderated tributary fed more frequently and consistently which resulted in larger fish. Similarly in the Betsie River watershed, larger juvenile steelhead were consistently observed in the Little Betsie tributary and in some years, movement from the mainstem into the tributaries seemed likely.

Steelhead smolt production is highly variable in some cases. Production of smolts in the Little Manistee River ranged from 11,845 to 86,425 smolts per year, yet a consistent number of age-1 parr were produced each year (Seelbach 1993). Huron River, tributary to Lake Superior, is in a harsher winter environment, but is a stream similar in size to the Little Betsie. This stream was found to produce between 1,031 and 9,141 steelhead smolts or alternately, 46 - 262 smolts/ha (Seelbach and Miller 1993). In contrast, the Betsie River produced a limited number of smolts, 1,125 +/- 1,441 - 2,096 +/- 716, but the abundance estimates were fairly consistent among years. Density estimates for smolt production from the Betsie River watershed were less than half of the Huron River estimates, ranging from 11.9 to 22.0 smolts/ha.

When compared with high quality trout streams, the production of steelhead in the Betsie River is very limited, yet historically this population has supported a popular steelhead fishery. Because the watershed is recovering from a major system disruption as a result of Thompsonville Dam failure in 1989, the current production estimates may underestimate prior production or future potential in the mainstem Betsie River.

After a similar experience with a dam collapse in the Pigeon River, Michigan, high silt loadings and sand introduction reduced the trout population (< 200 mm) by 52% (Alexander and Ryckman 1986). Suspended solids have been shown to cause sub-lethal stress effects in yearling steelhead (Redding et al. 1987). In the Betsie River, in addition to the initial impact of Thompsonville Dam failing, stream banks continue to erode and contribute sand which is highly mobile and observable as bedload movement during short time frames (Newcomb, unpublished data). This mobile sand bedload may be acting to suppress invertebrate populations (Alexander and Hansen 1986) and in concert with high temperatures, this could result in metabolic limitations for the population of steelhead parr in the main channel. Mean maximum summer water temperatures appeared to limit the distribution of juvenile steelhead throughout the watershed. Age-1 fish in particular showed a stronger relationship between maximum summer temperature and site densities. These results are similar to Roper et al. (1994) and are expected given, the ease of fish movement throughout the Betsie River. For example, at site 2, few age-1 steelhead were found in July, yet in October 1994 and 1995, large numbers of age-1 wild and hatchery fish were found here. This site is 10 km upstream from the hatchery stocking location and from areas of significant densities of age-1 parr. Spawning activity and steelhead redds were observed in this upper reach, yet few age-0 parr were captured here in July.

In the drought summer, 1995, summer temperatures were greatly increased throughout the watershed. This year also had the largest age-0 year class measured in the 4 years with a very low mortality estimate for summer to fall of 1995. Parr mean length in the fall for age-0 fish was smaller than lengths measured in 1994 and larger for age-1 parr. Although the exact mechanisms for this observation are not known, it may be that either density dependent factors limited the growth of age-0 fish or that growth was limited by the high metabolic costs of surviving in warm water. On the other hand, a larger number of age-1 parr reside in the Little Betsie River and Dair Creek, which approached the upper optimal growth limits without going above and incurring the higher metabolic costs.

Although, summer temperatures may limit distribution in the Betsie River watershed, winter effects may limit smolt abundance and cohort size. In studying a Michigan stream, Kocik (1992) found mortality rates (Z) of 1.07 during the growing season and higher winter rates of 1.57 for age-0 steelhead. His results compare favorably with the mortality rates in the Little Betsie River for age-0 steelhead which average 1.51 and results from the Betsie River as annual instantaneous rates for the entire watershed ranged from 0.71 to 1.81 with a mean of 1.14. Early winter acclimatization to cold temperatures has been shown to have a large influence on juvenile salmonids due to physiological limitations in early winter (Cunjak 1988). Furthermore, the more dramatic and sudden the winter cooling the greater the negative influence on the fish and this may give insight to the differences in mortality rates observed in the tributaries, where groundwater moderates the rapidly cooling air temperature, versus the mainstem Betsie River. Areas influenced by groundwater may be the key to winter habitat throughout the Betsie River watershed and those areas are confined to the tributaries and the main channel reach between sites 5-8.

Winter microhabitat may also be limiting in the Betsie River watershed. The important winter habitats observed in other streams such as cobble-boulder rubble along stream margins (Everest and Sedell 1983, Meyer and Griffith 1997) are limited in the Michigan watershed. Boulders and cobble are rare anomalies and woody debris along stream margins is really the only form of complex habitat available (Newcomb, unpublished data). Complex woody debris has been shown to be important to overwintering steelhead (Heifetz et al. 1986), the woody debris in the Betsie Main channel is not abundant. The absence of complex woody debris can be attributed in part to the logging history of the watershed that has left few old stands in the riparian zone to contribute as windfall and to clearing activities for canoe passage.

Other studies on the effects of winter severity on juvenile salmonid abundance have had mixed results. Overwinter mortality in the Little Manistee River ranged from 13 to 90% for juvenile steelhead (Seelbach 1987). In the Au Sable River, Michigan, Nuhfer et al. (1994) could not find a significant relationship between standing stocks of age-0 brown trout and winter severity as an index of air temperature. However, they did not analyze any older age-classes and the winter occurred during the egg incubation phase.

The effects that adult returns or broodstock size has on the population of juvenile steelhead in the Betsie River is unknown. There are no recent surveys to estimate fish harvest or return. In the late 1980's, creel harvest rates were estimated to range between 1,000 and 3,000 steelhead per year (Rakoczy and Rodgers 1987, 1988, 1990). However, the adult spawning population or total numbers in the return was not surveyed.

Conclusions

The Betsie River watershed is limited in the production of wild steelhead when compared with other steelhead producing streams. Although densities of juvenile steelhead vary both spatially and temporally throughout the watershed, consistent numbers of smolts are produced. Tributaries are a major component to the overall production of steelhead in this river that can be thermally marginal for trout and winter temperatures appear to influence mortality rates which are especially large for older fish. By the use of a watershed approach to assessing production, we were able to quantify areas critically important for steelhead based on thermal limitations and parr distribution.

Acknowledgments

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Table 1. Sampled reach characteristics in the Betsie River watershed.

Reach & Sites	Mean July Discharge (m^3/s)	Mean Channel Width (m)	Mean Channel Depth (m)
Upper Betsie River (1-4)	2.2	14.4	0.4
Lower Betsie River (5-8)	5.5	17.1	0.5
Little Betsie River (9-10)	0.5	6.7	0.3
Dair Creek (11-12)	0.4	5.5	0.2
Small Tributaries (12-13)	0.1	1.7	0.1

Table 2. Air temperature for summer and winter (°C) from the Cadillac weather station.

Year	Summer Mean Temperature (^oC) (Jun-Jul-Aug)	Winter Mean Temperature (^oC) (Dec-Jan-Feb)*	# Days < -12^{o}C
1993	18.6	-7.9	8
1994	18.1	-11.8	29
1995	20.4	-6.3	9
1996	18.0	-8.8	20

* December is from the prior year

Table 3. Water temperature for summer and winter mean temperature in the Betsie River at Homestead Weir and Little Betsie River, 1993-1996.

	Summer Mean Temperature(°C)		Winter Mean Temperature (°C)	
Year	Little Betsie	Betsie	Little Betsie	Betsie
1993	16.0	18.3	no data	no data
1994	15.9	17.6	1.0	0.9
1995	17.5	19.0	1.9	1.6
1996	16.0	17.8	0.7	0.4

Table 4. Sampled reach water temperature characteristics in the Betsie River watershed.

	Water Temperature (°C)			
	Summer		Winter	
Reach and Sites	Mean	Max	Mean	Min
Upper Betsie River (sites 1-4)	20.9	26.7	0.7	-1.1
Lower Betsie River (sites 5-8)	18.4	23.3	1.03	-0.3
Little Betsie River (sites 9-10)	16.2	20.6	1.14	-0.4
Dair Creek (sites 11-12)	14.7	18.9	1.41	-0.3
Small Tributaries (sites 12-13)	7.2-12.8[1]			

[1] periodic measurements during the summer

Table 5 Age structure and watershed yield of wild steelhead smolts migrating from the Betsie River watershed, May-June, 1993-1996.

Year	Total	% Age-1	% Age-2	%Age-3	Smolts/Ha
1993	2,096 ± 716	54	46	0	22.2
1994	1,847 ± 1,152	48	44	8	19.6
1995	1,534 ± 1,804	53	40	7	16.3
1996	1,125 ± 1,441	78	21	2	11.9
MEAN	**1,651**	**58**	**38**	**4**	**17.5**

Table 6. Density estimates and 95% confidence intervals for age-0 and age-1 steelhead parr at sites sampled by electrofishing and depletion methods throughout the Betsie River watershed, 1993-1996.

	SAMPLING SITES													
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
SUMMER (AGE-0)														
1993	0	0	-	-	157.5	3.1	485.7	180.6	350.0	-	1600.0	2200.0	-	1000.0
					±89.6	±3.5	±303.0	±31.9	±20.7		±339.5	±195.3		±86.9
1994	0	0	0	0	25.0	58.7	499.0	38.9	1973.8	1327.6	1050.0	1800.0	1250.0	523.0
					*	±90.9	±21.5	±39.2	±87.1	±183.0	±72.7	±21.6	±43.3	±306.4
1995	0	80.0	16.7	9.1	85.3	360.9	1378.4	175.0	1532.1	360.6	1167.0	3090.9	1350.0	757.1
		±84.3	±4.4	±4.2	±119.0	±80.8	±73.3	±53.2	±30.4	±139.4	±1583.9	±352.3	±63.2	±110.5
1996	0	0	0	-	12.3	41.7	32.5	11.1	157.1	61.5	369.2	2775.0	800.0	2296.9
					±32.9	±36.5	*	*	±11.4	±25.4	±18.8	±273.7	±35.0	±89.6
SUMMER (AGE-1)														
1993	0	0	-	-	22.5	0	709.8	18.1	1200.0	-	0	0	-	200.0
					±12.8		±442.8	±3.2	±70.8					±17.4
1994	0	0	0	0	8.3	39.2	69.9	0	943.0	113.3	0	0	1750.0	31.4
					*	±30.9	±3.0		±79.9	±15.6			±393.9	±105.0
1995	0	0	8.3	36.4	24.4	68.2	75.1	19.4	978.8	106.1	166.7	103.0	750.0	108.2
			±2.2	±16.9	±34.0	±15.3	±4.0	±5.9	±19.6	±41.0	±115.4	±11.7	±35.1	±15.7
1996	0	0	7.7	-	0	16.7	71.5	16.7	257.1	23.1	138.5	102.8	600.0	423.1
			*			*	±1.6	*	±18.7	±9.5	±7.1	±10.1	±26.3	±16.5
FALL (AGE-0)														
1994	0	13.5	0	0	145.8	15.4	1676.5	-	1421.9	970.2	250.0	800.0	1326.5	714.3
		±8.0			±75.8	*	±56.8		±135.0	±59.5	*	±77.4	±128.2	±10.9
1995	0	0	8.3	-	25.0	234.2	1399.4	-	1320.0	500.0	400.0	700.0	650.0	1000.0
			±8.2		±2.8	±39.3	±63.4		±25.1	±15.5	±92.9	±77.4	±21.0	±28.8
FALL (AGE-1)														
1994	0	13.5	0	0	31.3	7.7	111.8	-	634.4	14.9	0	0	1071.4	0
		±8.0			±16.3	*	±3.8		±60.2	±0.9			±103.6	
1995	0	40.0	0	-	33.3	81.1	138.0	-	700.0	128.6	0	0	850.0	83.3
		±7.1			±3.7	±13.6	±6.3		±13.3	±4.0			±27.4	±2.4

* indicates no variance calculated, all fish caught on first pass

Table 7. Density of age-0 and age-1 steelhead parr in the upper (1-4) and lower (5-8) reaches of the Betsie River, October 1994-1995.

Year	Age-Class	Upper River	Lower River
1994	Age-0	31.9 ± 15.3	846.0 ± 28.4
	Age-1	9.0 ± 3.6	59.8 ± 1.9
	Age-2	1.4 ± 0.8	0
1995	Age-0	8.3 ± 2.2	816.8 ± 37.3
	Age-1	18.3 ± 2.0	109.5 ± 7.5
	Age-2	7.1 ± 0.9	0

Table 8. Watershed abundance estimates and 95% confidence intervals for age-0, age-1 and age-2 steelhead parr calculated from stratified reach estimates throughout the Betsie River watershed, July, 1993-1996.

Year of Sampling	Age-0 Parr	Age-1 Parr	Age-2 Parr
1993	18,795 ± 27,275	18,485 ± 37,708	0
1994	20,569 ± 13,778	8,357 ± 4,924	976 ± 549
1995	32,896 ± 17,081	7,621 ± 3,953	153 ± 16
1996	9,130 ± 4,789	4,505 ± 1,499	0

Table 9. Annual, winter, and summer instantaneous mortality rates (Z) for steelhead parr cohorts observed in the Betsie River watershed, 1993-1996. The annual mortality rate includes an adjustment for the cohort's emigrating smolts.

	Mortality		
Year	(age-0 to age-1)	(age-1 to age-2)	(age-2 to age-3)
ANNUAL			
1993-1994	0.710	2.395	1.881
1994-1995	0.892	2.489	2.817
1995-1996	1.810	3.576	3.507
MEAN	**1.137**	**2.820**	**2.735**
JULY-OCTOBER			
1994	3.839	1.215	2.166
1995	0.185	*	*
OCTOBER-JULY			
1994-1995	1.842	3.212	1.395
1995-1996	2.396	4.633	4.396

*indicates more fish captured in October than in July

Table 10. Annual instantaneous mortality rates (Z) throughout the Betsie River watershed without adjustment for outmigrating smolts, 1993-1996.

	Mortality Age-0 to Age-1	Mortality Age-1 to Age-2
Betsie River		
1993-1994	2.260	**
1994-1995	0.987	**
1995-1996	2.795	**
MEAN	**2.014**	
Little Betsie River		
1993-1994	*	2.056
1994-1995	1.105	**
1995-1996	1.910	**
MEAN	**1.508**	
Dair Creek		
1993-1994	0.116	2.545
1994-1995	0.726	3.265
1995-1996	0.722	**
MEAN	**0.521**	

* larger estimate of age-1 than age-0
** no observations of age-2 parr

Table 11. Mean lengths and 95% confidence intervals for age-0 and age-1 steelhead parr sampled from four reach categories throughout the Betsie River watershed, 1993-1996.

	CHANNEL			
Year	Betsie River	Little Betsie River	Dair Creek	Small Tributaries
SUMMER				
AGE-0				
1993[1]	55.8 ± 8.4	77.0 ± 12.2*	80.6 ± 10.6*	53.2 ± 5.8
1994	50.9 ± 7.3	62.4 ± 6.8	47.2 ± 8.0	49.7 ± 6.2
1995	52.9 ± 6.4	61.7 ± 6.0	48.5 ± 9.4	47.6 ± 7.5
1996	50.9 ± 6.5	52.1 ± 4.5*	43.8 ± 7.4	44.6 ± 7.2
AGE-1				
1993[1]	155.2 ± 8.4*	148.1 ± 8.7	128.0 ± 6.2	0 age-1 parr
1994	137.8 ± 8.2	145.9 ± 8.2	149.6 ± 8.0	0 age-1 parr
1995	152.3 ± 8.8*	152.8 ± 8.9	132.1 ± 8.7	127.3 ± 11.0
1996	138.3 ± 10.0	168.4 ± 9.5*	132.3 ± 8.5	118.5 ± 6.3
FALL				
AGE-0				
1994	89.1 ± 7.4*	94.4 ± 7.3*	73.9 ± 7.9	74.2 ± 7.7
1995	83.3 ± 6.6	87.2 ± 6.8	71.2 ± 6.9	67.5 ± 7.7
AGE-1				
1994	154.4 ± 8.5	152.9 ± 7.3	139.1 ± 9.2	0 age-1 parr
1995	157.5 ± 10.8	166.2 ± 10.1*	150.2 ± 10.3	0 age-1 parr

[1] Sampling dates 10 days later in the summer than 1994-1996.

* Indicates a significant difference ($P < 0.05$) within the reach among the years for the age-class.

Table 12. Comparison of steelhead parr densities in select streams.

General Location	Stream	Mean Q (cms)	Total Steelhead Parr/ha	Density per hectare		
				Age-0	Age-1	Age-2
Southern Michigan	Sand Creek	0.14	1,536	1,045	476	15
	Silver Creek	0.14	1,818	436	1,345	36
Ontario Canada	Normandale Creek	0.14	600 - 2,200			
Northern Michigan	Pine Creek	0.60	4,500			
	Little Manistee	5.0-6.0		2,295	663	10
	Little Betsie	0.5		764	604	19
	Dair Creek	0.4		1,123	508	25
	Betsie River	5.5		124	46	0

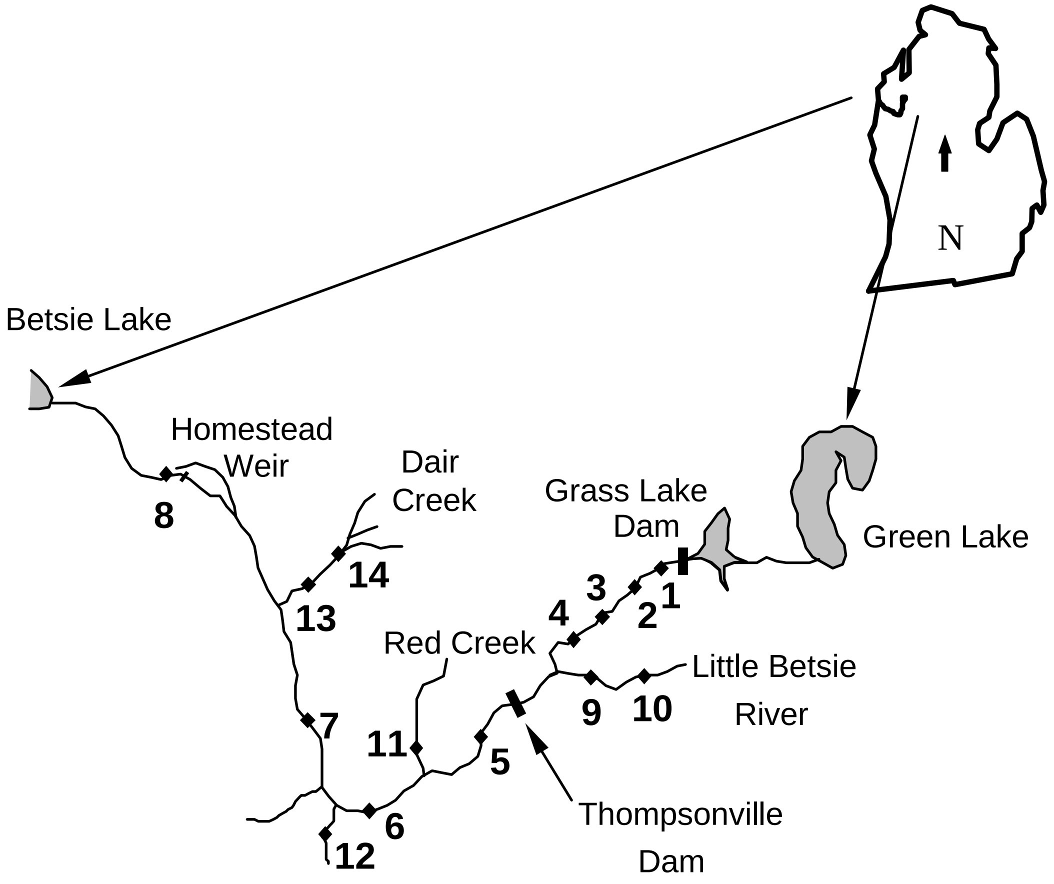

Figure 1. Sampling sites for the electrofishing throughout the Betsie River watershed, Michigan, 1993-1996.

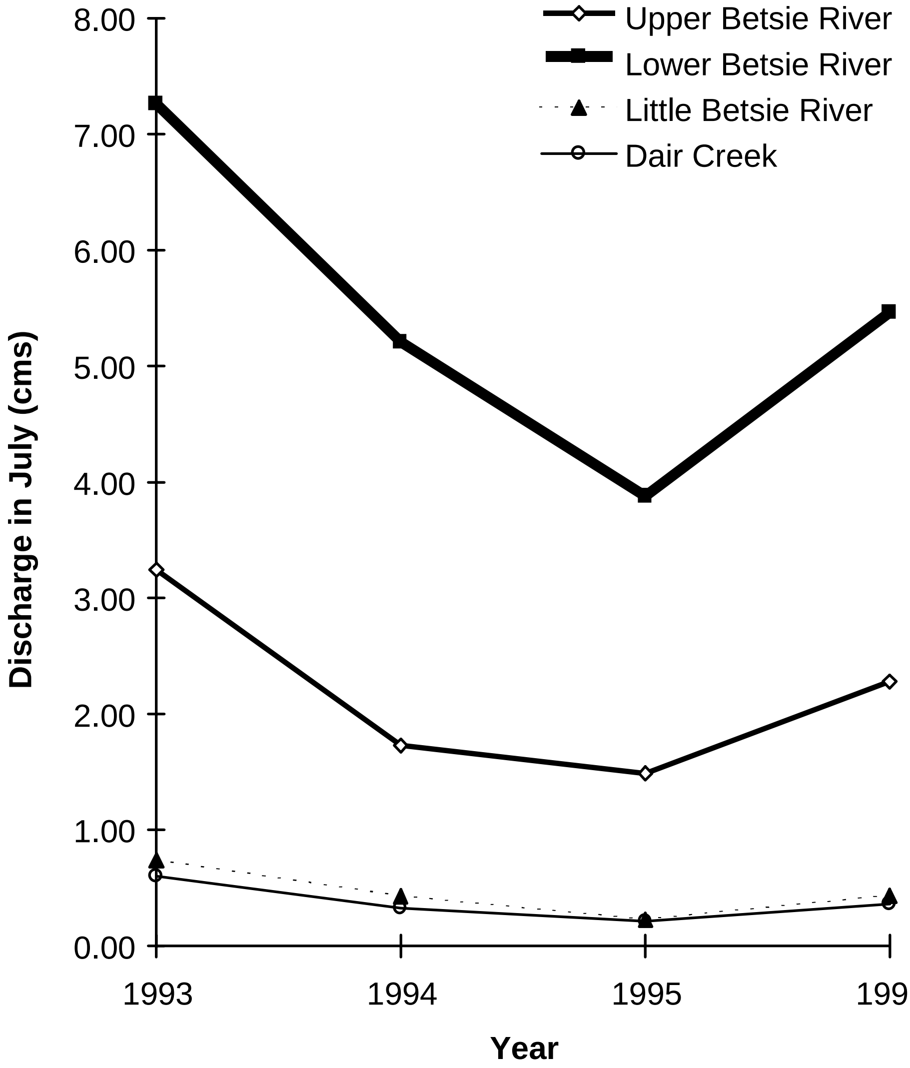

Figure 2. Mean discharge measured in July at sampling reaches in the Betsie River Watershed, 1993-1996.

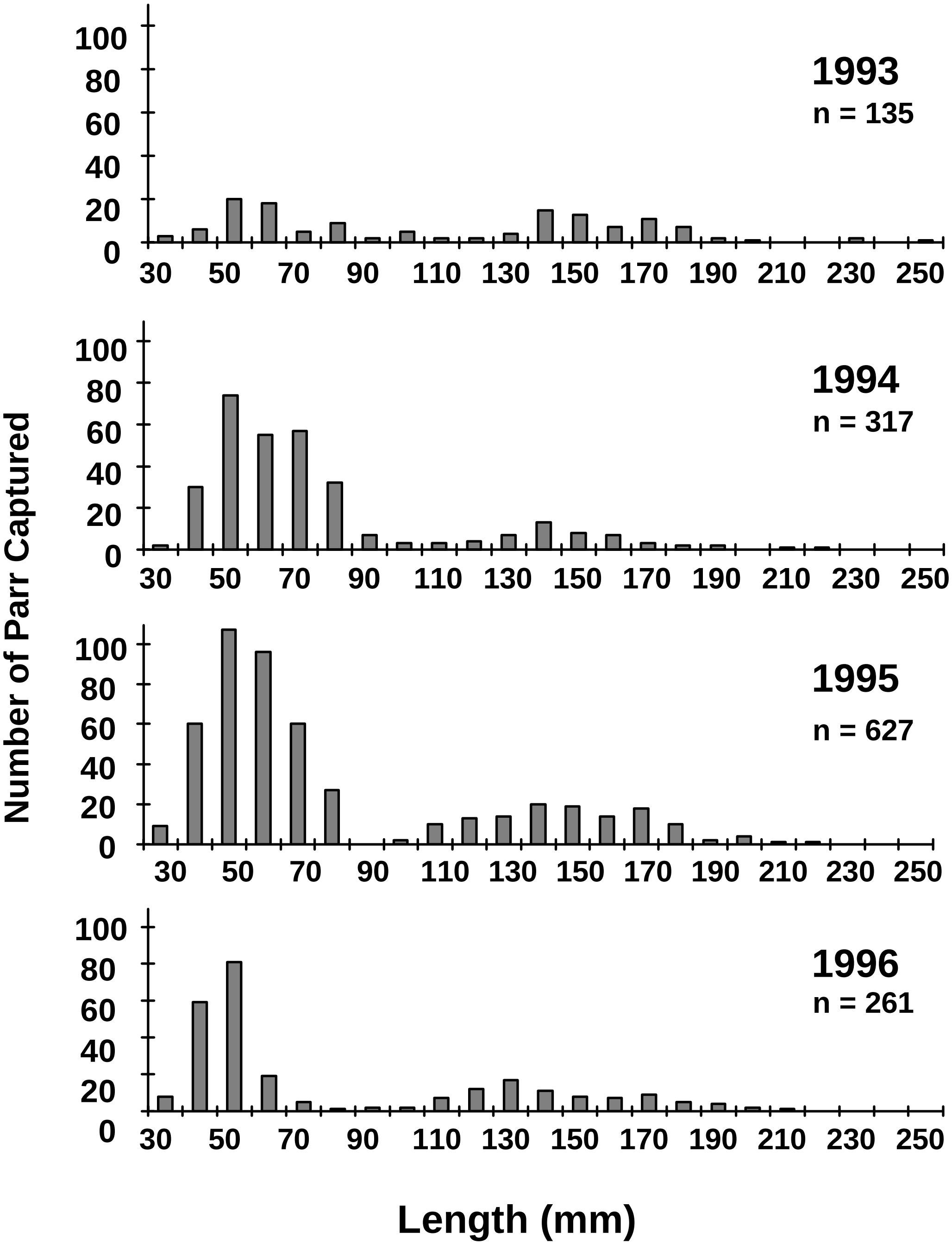

Figure 3. Length-frequency distribution of steelhead parr captured in July in the Betsie River watershed, 1993-1996.

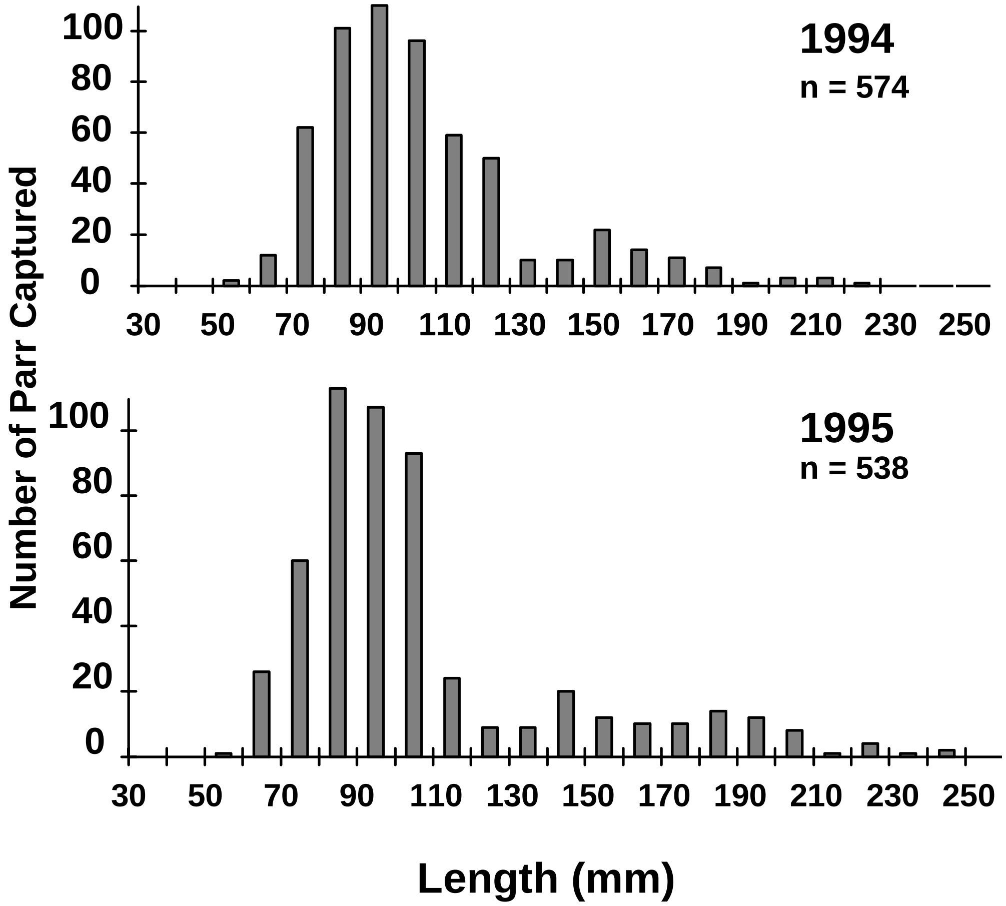

Figure 4. Length-frequency distribution of steelhead parr captured throughout the Betsie River watershed in October, 1994-1995.

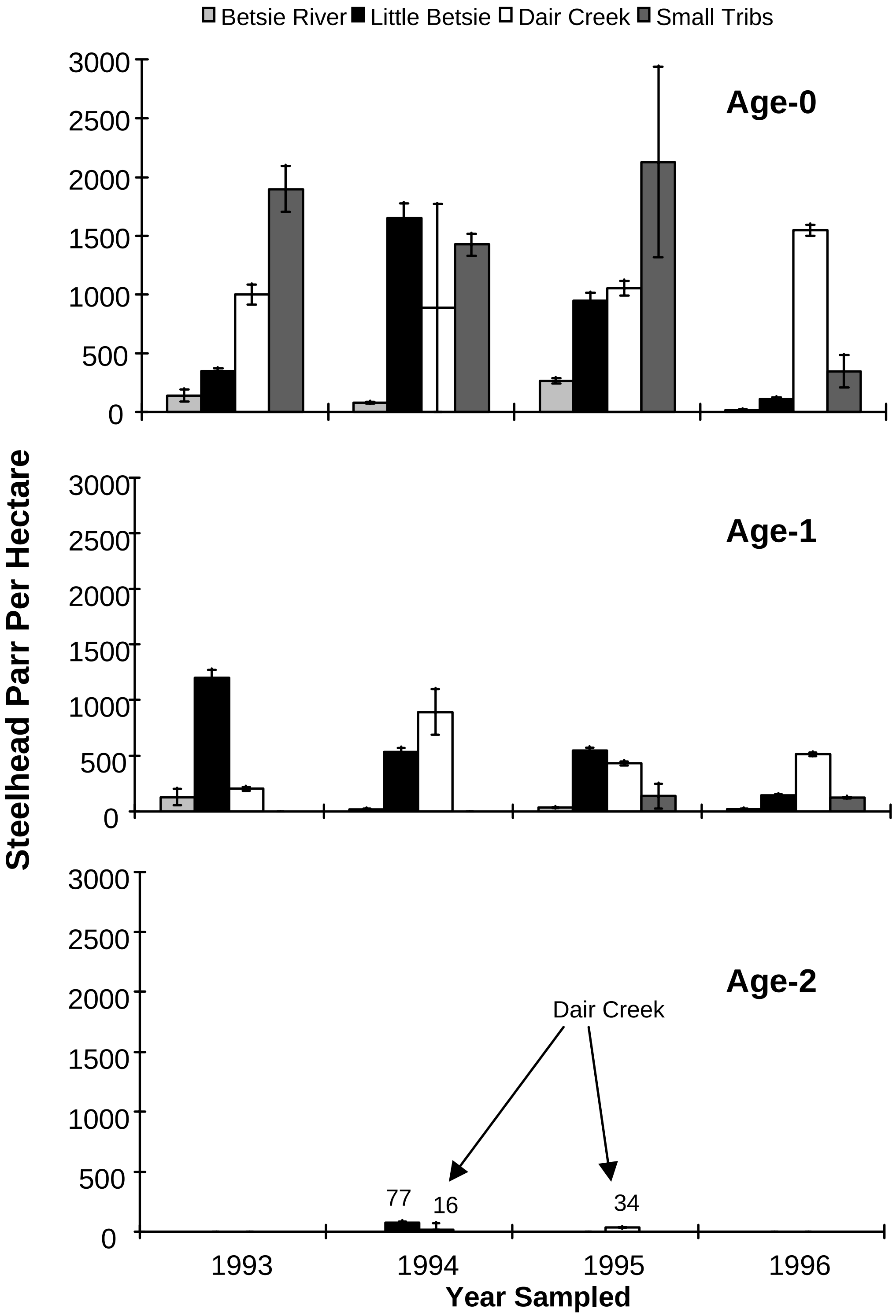

Figure 5 . Comparison of age-0, age-1, and age-2 steelhead parr densities between the Betsie River and its tributaries, July, 1993-1996.

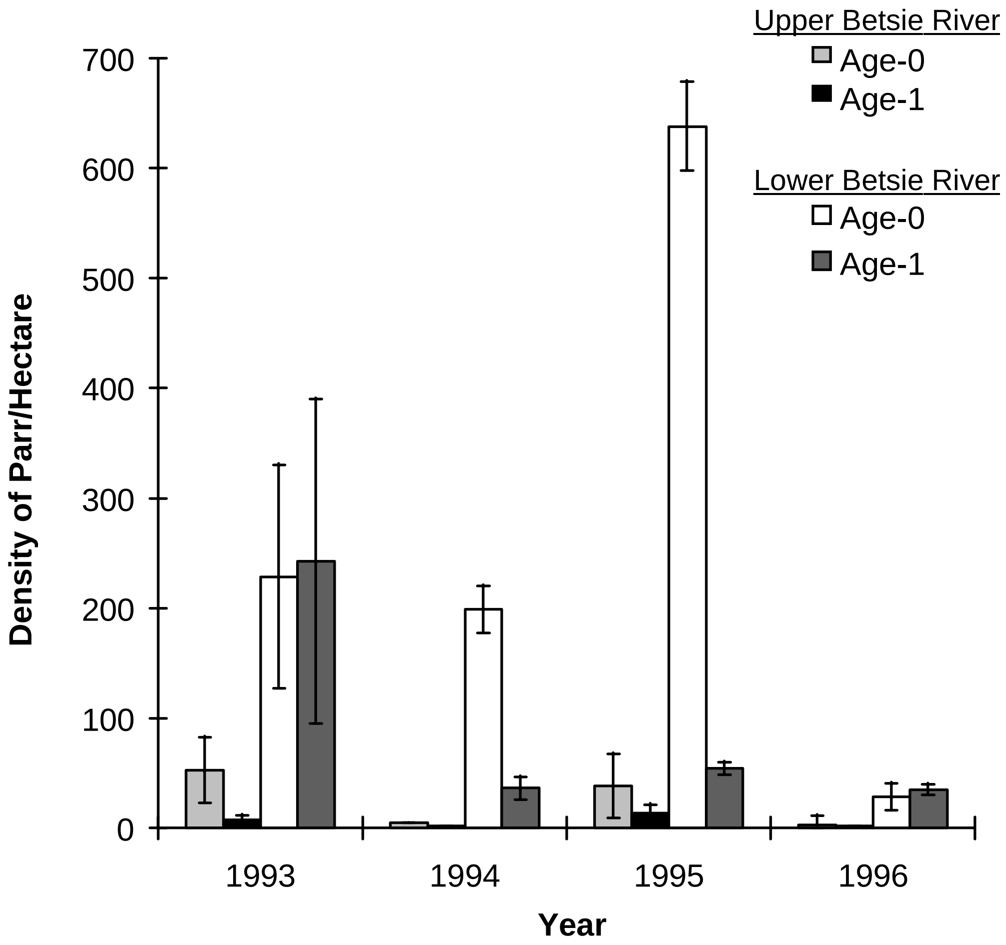

Figure 6. Comparison of the desnities of age-0 and age-1 steelhead parr in the upper and lower reaches of the Betsie River, 1993-1996.

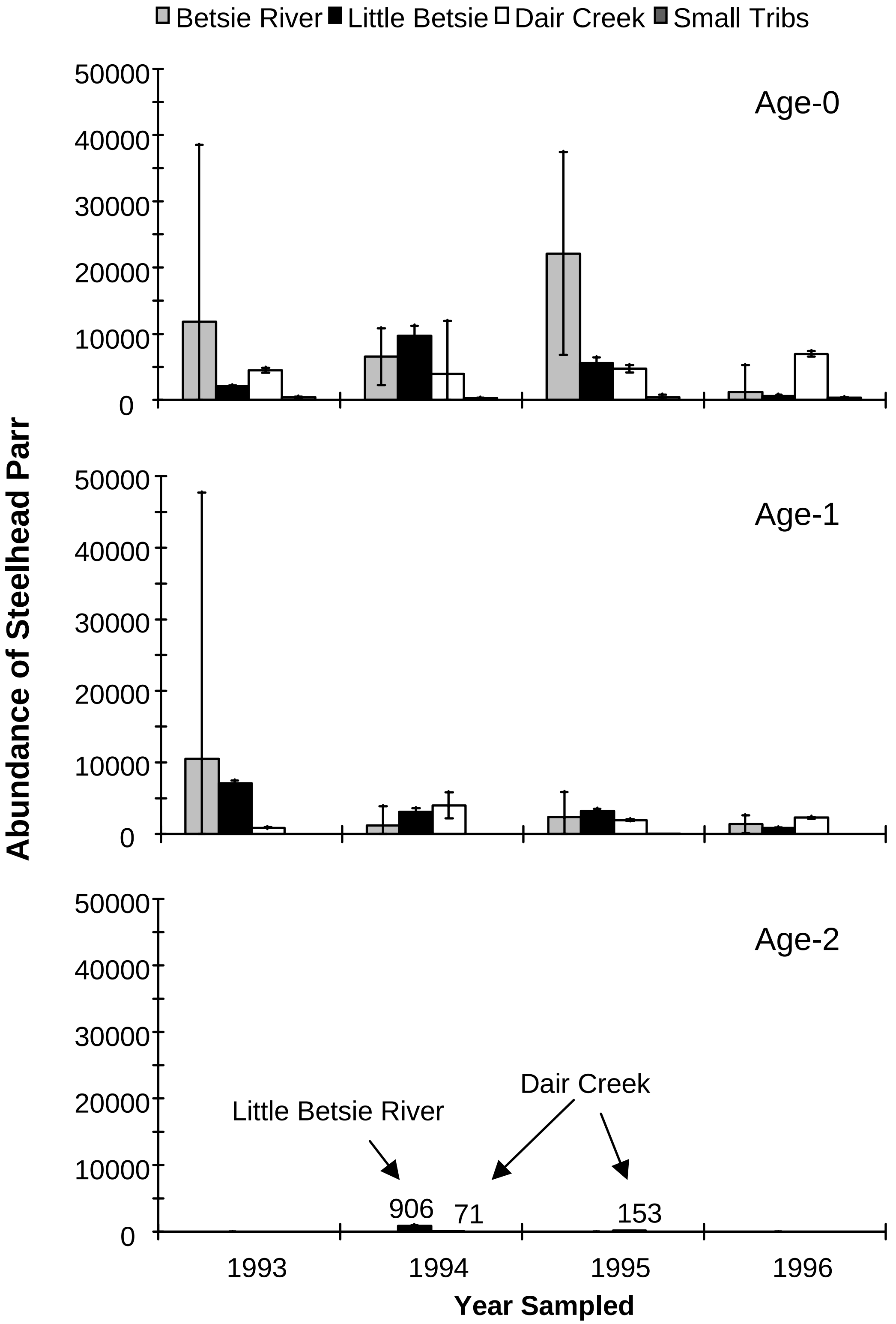

Figure 7. Estimate of abundance of steelhead parr in 4 reaches throughout the Betsie River watershed, July, 1993-1996.

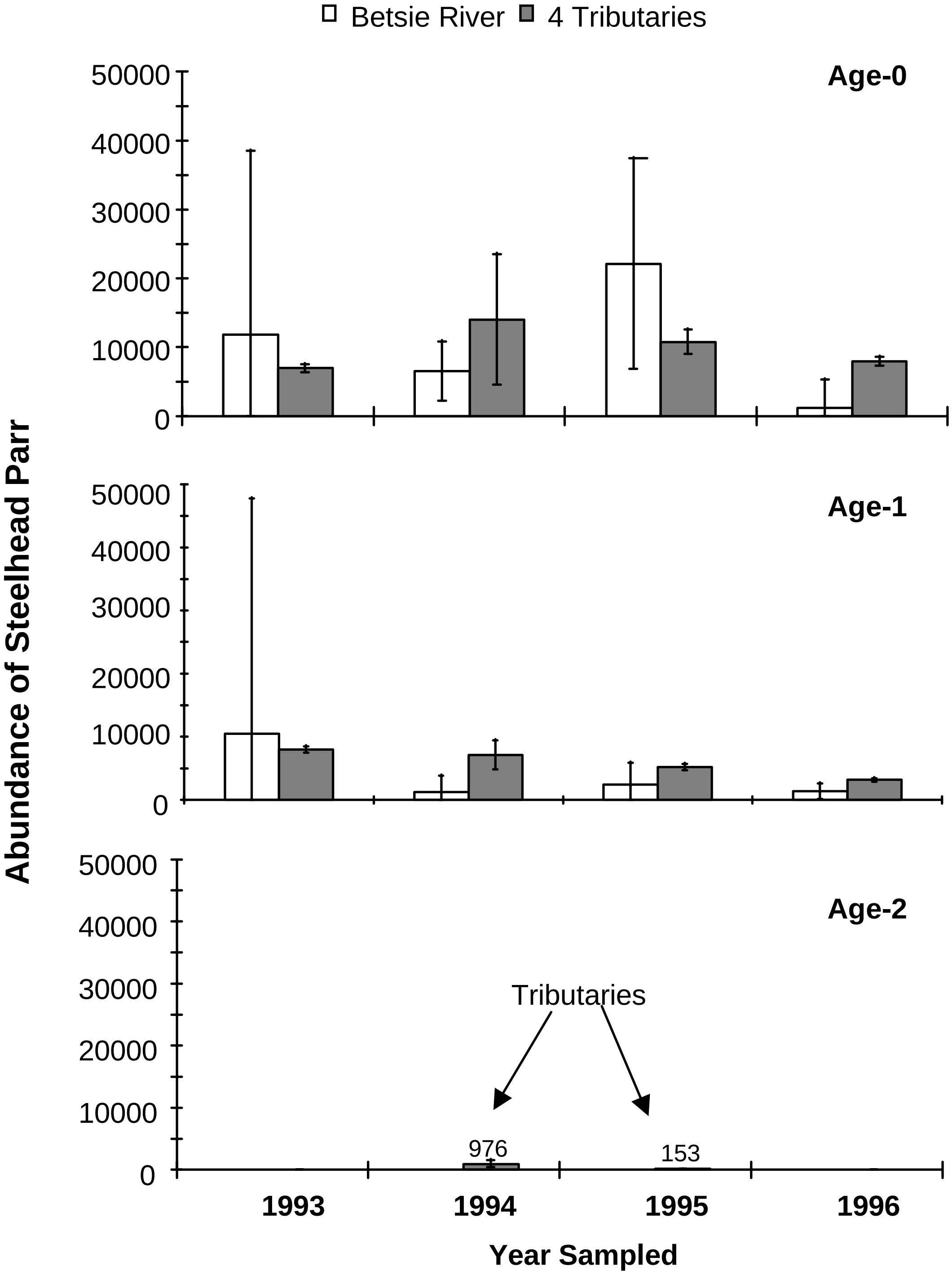

Figure 8. Comparison of abundance of steelhead parr in the Betsie River and the four tributaries that were sampled throughout the watershed, July, 1993-1994.

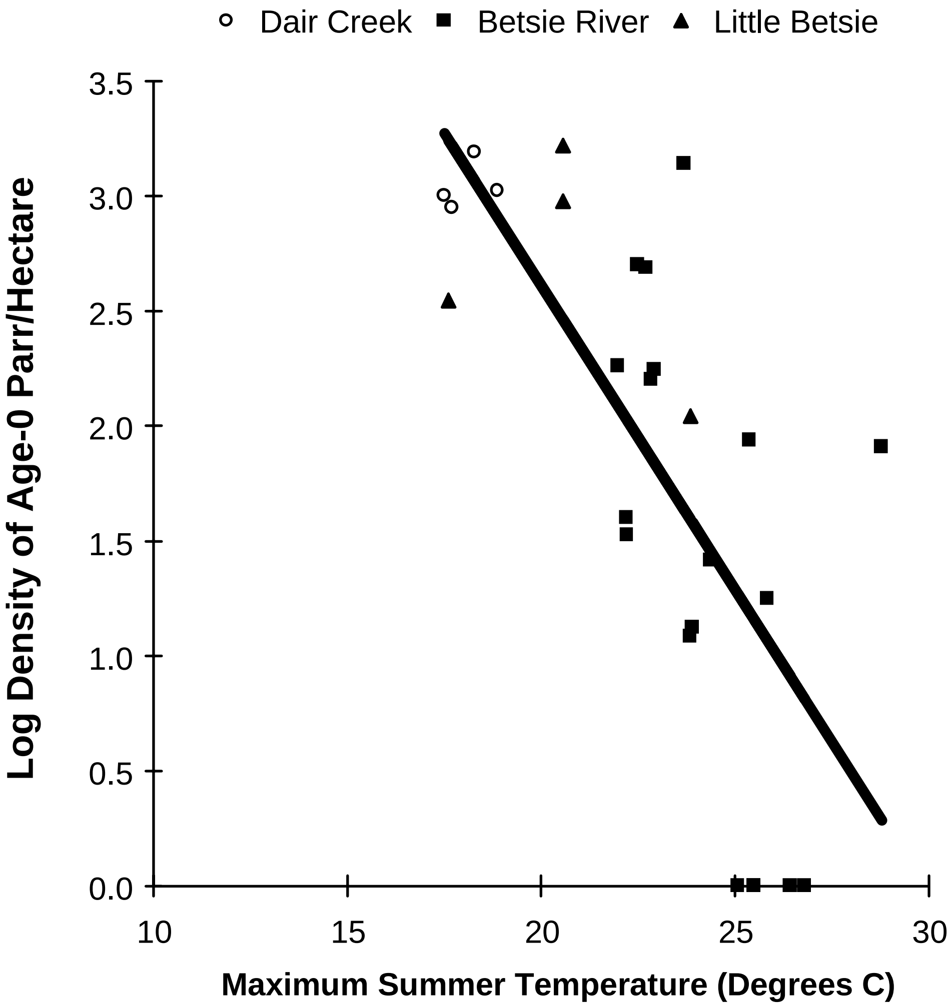

Figure 9. Correlation between the density of age-0 steelhead parr and the maximum summer water temperature at sites throughout the Betsie River Watershed, 1993-1996 (adjusted $r^2 = 0.4981$, $p = 0.00002$).

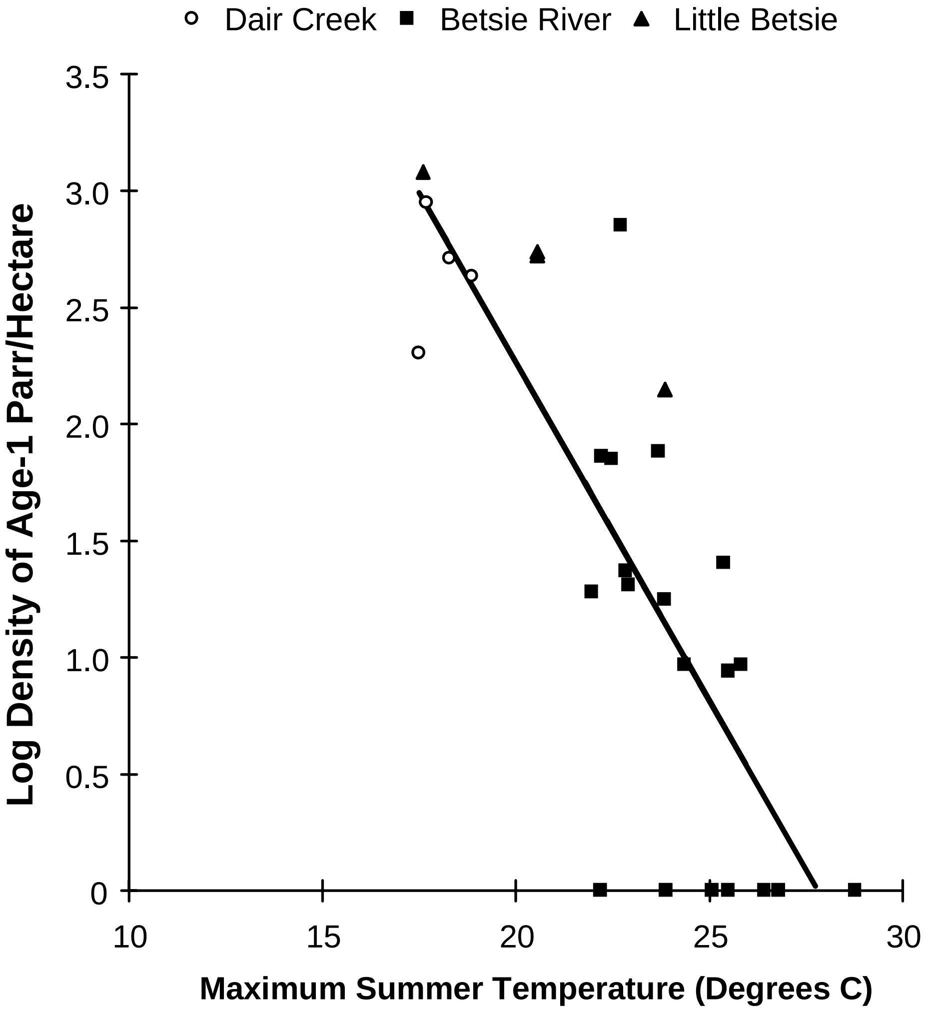

Figure 10. Correlation between the density of age-1 steelhead parr and the maximum summer water temperature at sites throughout the Betsie River Watershed, 1993-1996 (adjusted $r^2 = 0.6225$, $p = 0.000007$).

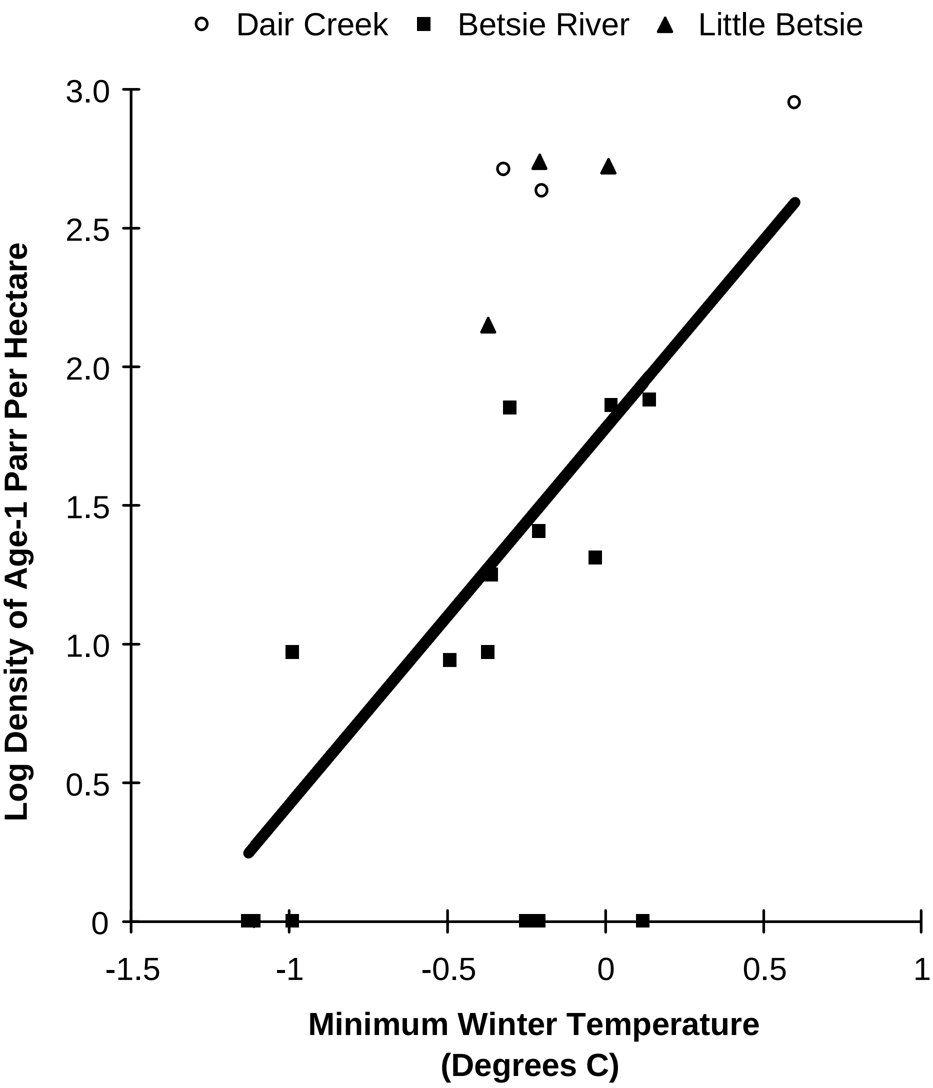

Figure 11. Correlation between the density of age-1 steelhead parr and the minimum water temperature at sites throughout the Betsie River Watershed, 1993-1996 (adjusted $r^2 = 0.3391$, $p = 0.0275$).

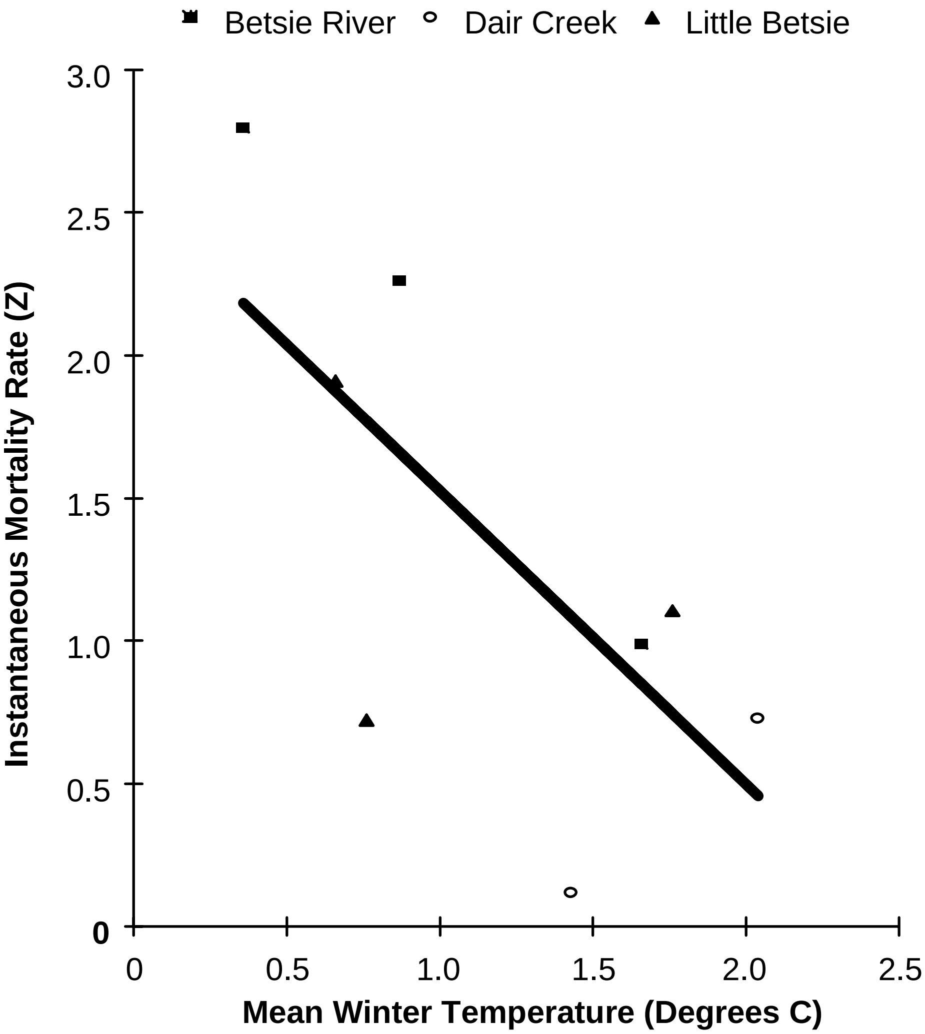

Figure 12. Correlation between mean winter temperature and the annual mortality rate for steelhead parr (age-0 to age-1) at sites throughout the Betsie River Watershed, 1993-1996 (adjusted $r^2 = 0.389$, $p = 0.0581$).

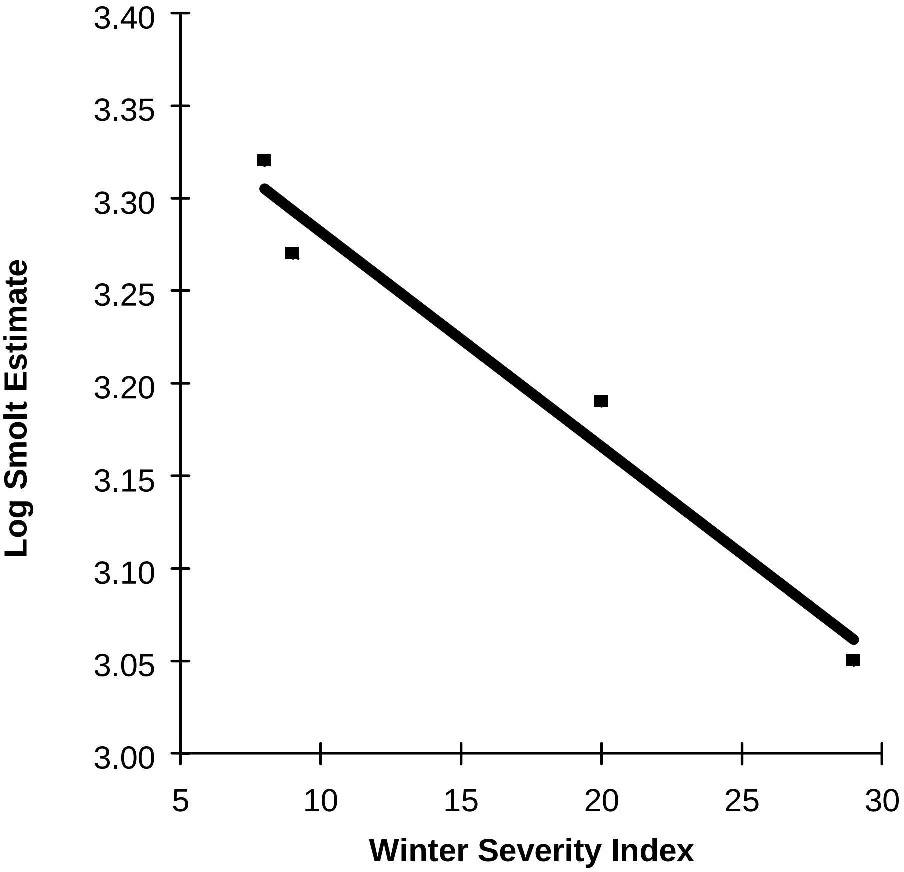

Figure 13. Correlation between the winter severity index (number of days when air temperature is less than -12^{0}C) and the estimate of smolts leaving the Betsie River Watershed, 1993-1996 (adjursted $r^2 = 0.946$, $p = 0.018$)

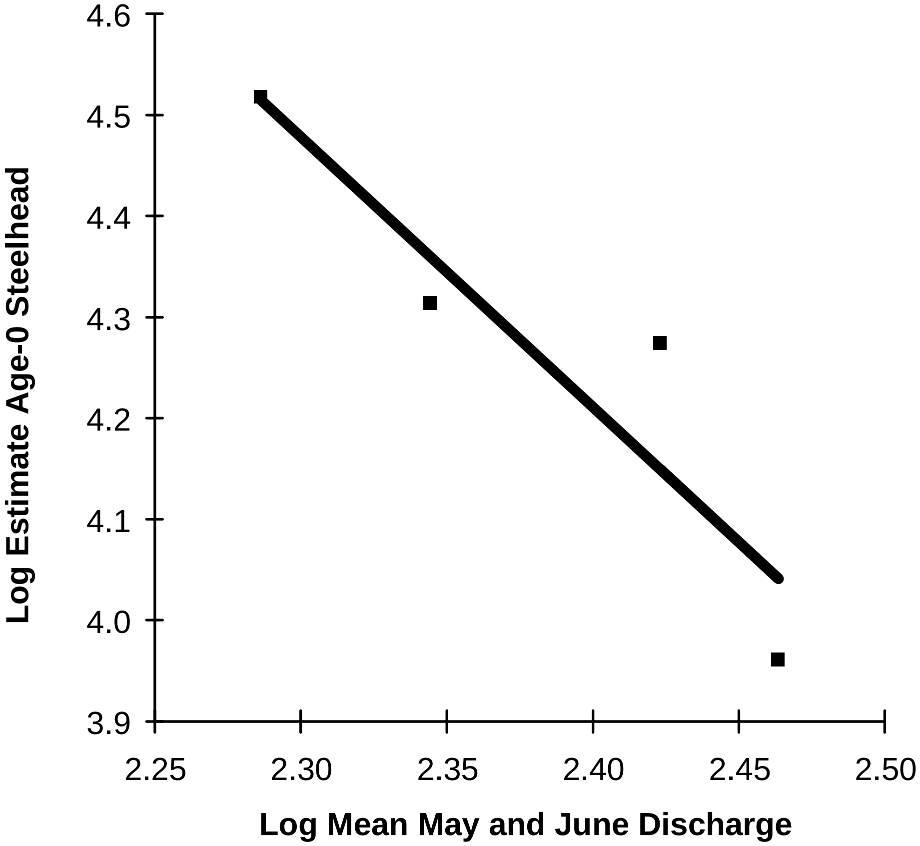

Figure 14. Correlation between the abundance of age-0 steelhead in July and the mean May and June discharge in the Betsie River watershed., 1993 - 1996 (adjusted $r^2 = 0.771$, $p = 0.079$).

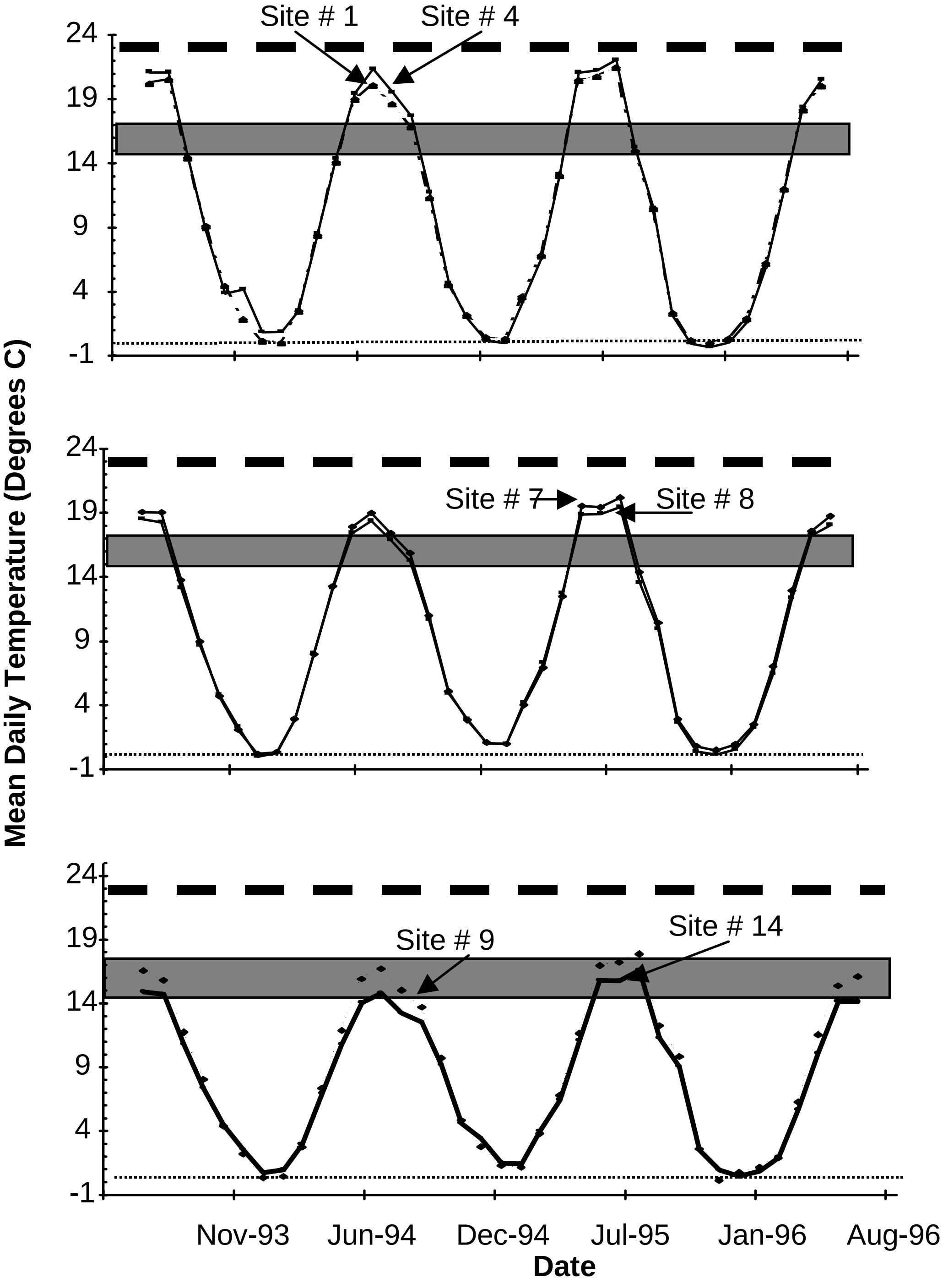

Figure 15. Comparison of mean monthly water temperature among 6 sites in the Betsie River watershed. The gray shaded area respresents the optimal growth range for juvenile steelhead, the heavy dashed line is the upper zero growth level (23^0 C), the light dashed line is the lower lethal level (0^{0}C).

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