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Rainbow Trout in a Regulated River below Glen Canyon Dam, Arizona, following Increased Minimum Flows and Reduced Discharge Variability

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Abstract.—We examined the effects of dam operation on the relative abundance and relative condition of rainbow trout *Oncorhynchus mykiss* captured by electrofishing between 1991 and 1997 in the Lee's Ferry tailwater below Glen Canyon Dam, Arizona. Higher minimum, higher mean, and more stable flow releases from the dam after 1991 provided conditions that supported greater relative abundance of rainbow trout. Though the relative abundance of most length-classes increased following the onset of a stabilized flow regime, relative condition declined, particularly in large rainbow trout ($\geq$305 mm). Correlation analyses suggested that the small rainbow trout ($<$305 mm) were more strongly influenced by physical factors (flow variation, mean discharge, and water temperature) than the large trout ($\geq$305 mm). However, the relative condition of small trout was negatively correlated with that of all trout, and the condition of trout 305–405 mm in length was negatively correlated with the relative abundance of trout within this length category, suggesting food limitation or density-dependent influences on physiological well-being. Our findings enhanced the understanding of rainbow trout ecology in the Lee's Ferry tailwater by demonstrating that a stabilized flow regime provides conditions supportive of greater relative abundance.

Several studies have demonstrated that alterations of flow regimes in regulated rivers influence populations of warmwater fishes (Weisberg and Burton 1993; Travnichek et al. 1995; Bowen et al. 1998). Increased flows below hydroelectric power dams are frequently used to benefit lotic biota, but effects of this management action are not well understood (Weisberg and Burton 1993; Travnichek et al. 1995). A combination of higher minimum water releases and reduced discharge variability from hydroelectric power facilities have corresponded with increased densities of warmwater fishes (Travnichek et al. 1995), but it is possible the populations may have benefited from higher minimum flows alone (Weisberg and Burton 1993). Dams influence fish habitat (Bain et al. 1988; Scheidegger and Bain 1995; Bowen et al. 1998) and benthic biomass (Blinn et al. 1995; Stevens et al. 1997; Benenati et al. 1998), but their effects on rainbow trout *Oncorhynchus mykiss* populations are poorly understood.

Travnichek et al. (1995) found that warmwater fishes in a dam tailwater increased fivefold after increased minimum discharge and reduced fluctuation in flows (Travnichek et al. 1995). This suggests that a similar trend might be possible for rainbow trout following the stabilization of flow regimes. Increasing relative abundance of rainbow trout in cold dam tailwaters, however, may be paralleled by food base degradation, depression of fish growth, and smaller average fish size (Walters and Post 1993; Filbert and Hawkins 1995; Weiland and Hayward 1997). Moreover, several studies have indicated that dam operation and increased relative abundance of fish might be associated with length-specific responses to dam operation (Cada et al. 1987; Filbert and Hawkins 1995; Weiland and Hayward 1997).

The inception of higher minimum flows, greater mean discharge, and reduced diel fluctuation from Glen Canyon Dam after mid-1991 provided an opportunity to study changes in a rainbow trout population associated with this management action (U.S. Department of Interior 1995, 1996). Our objective was to examine temporal changes in the relative abundance and condition of rainbow trout in the cold dam tailwater following stabilization of the flow regime and to evaluate associations between dam operation and population indices.

Study Site

Glen Canyon Dam impounds the Colorado River in northcentral Arizona near the Arizona–Utah border. The dam construction formed Lake Powell,

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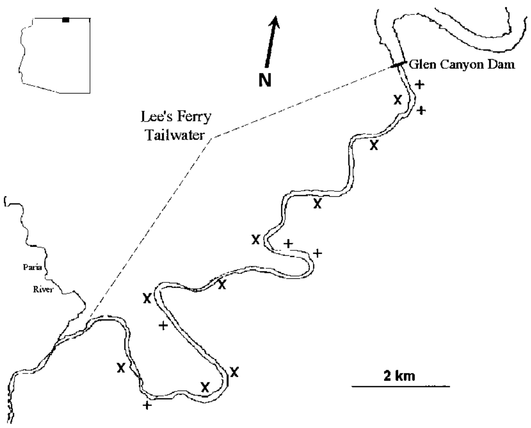

FIGURE 1.—Map of Lee's Ferry tailwater on the Colorado River below Glen Canyon Dam. Symbols indicate the locations of nine electrofishing transects sampled continually during 1991–1997 (X) and those that were sampled between 1991 and 1996 (+).

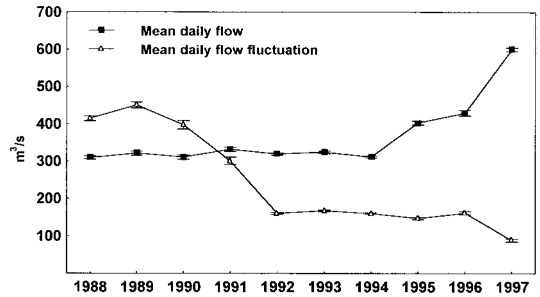

FIGURE 2.—Mean (±SE) annual daily flows and fluctuations from 1988 to 1997 of releases from Glen Canyon Dam, Colorado River.

a 653-km² meromictic reservoir. Hypolimnetic releases from the reservoir are clear and cold (Stanford and Ward 1991; Stevens et al. 1997). The Lee's Ferry tailwater extends between the dam at river kilometer (rkm) 25.5 and Lee's Ferry at rkm 0 (Figure 1). The tailwater is confined within a narrow, deeply incised canyon and has no perennially flowing tributaries. At a dam discharge rate of 426 m^3/s, mean depth of the 341-ha tailwater is 6.5 m and mean width is 135.6 m.

Nonnative rainbow trout are the most abundant fish in the dam's tailwater. Also present are comparatively abundant native flannelmouth sucker *Catostomus latipinnis* (McKinney et al. 1999a) and a small number of nonnative common carp *Cyprinus carpio.* The Arizona Game and Fish Department (AGFD) manages the tailwater as a recreational fishery. Between 1991 and 1997, the harvest of trout 406–558 mm (slot length) was prohibited, and the daily creel limit was limited to two trout outside this length.

Between 1988 and 1994, mean water releases from Glen Canyon Dam were approximately 300 m^3/s, increasing to about 600 m^3/s by 1997 (Figure 2). Daily water releases commonly fluctuated from less than 142 m^3/s to over 500 m^3/s during 1988–1991; minimum daily flows approached 85 m^3/s (McKinney and Persons 1999). After mid-1991, minimum releases from the dam were 142 m^3/s and mean daily fluctuations in flows declined more than 50% (Figure 2).

Methods

Field collections.—We captured rainbow trout in the Lee's Ferry tailwater (1991–1997) between dusk and dawn 2–4 times per year ($N = 23$) by single-pass electrofishing from an aluminum boat at 15 (1991–1996) or 9 (1997) randomly selected transects (Figure 1). Transect lengths averaged 0.6 km, and each was electrofished for approximately 33 min in February–April, July–September, and November–December throughout the study. We used a complex pattern of pulsed DC, applying 215 V and maintaining a 15-A average output to a 30-cm stainless steel anode system (Sharber et al. 1994). Fish were measured (total length [TL], mm), weighed (g), scanned for the presence of coded wire tags implanted since 1992 (stocked fish), and released.

The U.S. Bureau of Reclamation provided dam discharge data and the Grand Canyon Monitoring and Research Center provided water temperatures (°C) in dam draft tubes (S. Hueftle and W. Vernieu, personal communication). Angler catch rate, use, and trout-stocking data were taken from McKinney and Persons (1999), and estimated angler harvest data based on creel surveys were provided by AGFD (unpublished data).

Analytical procedures.—Four length categories (small fish: ranges, 0–151 mm and 152–304 mm; large fish: ranges, 305–405 mm and 406–558 mm), catch per minute, and relative condition factors for all trout) were compared among years and sampling locations using two-way analyses of variance (ANOVA). Length categories were selected for analysis based on the estimated age of small fish (0–151 mm = young of year; 152–304 mm = age 1; unpublished data), length at sexual maturity (≥305 mm; unpublished data), and slot length. Years were treated as fixed effects and sampling locations were treated as random effects. Because of fluctuating water levels and associated variation in physical variables (AGFD, unpublished data), sampling locations were not habitat-specific; how-

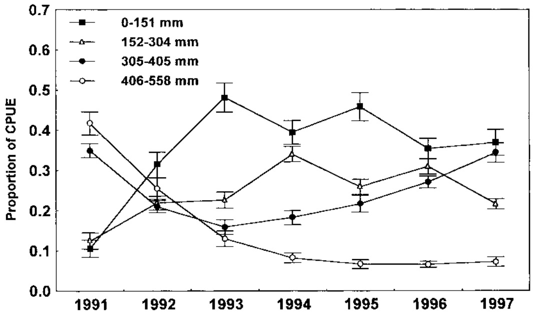

FIGURE 3.—Mean (±SE) proportion of the total electrofishing catch (CPUE = catch per minute) of rainbow trout of different lengths from 1991 to 1997 in the Lee's Ferry tailwater, Colorado River.

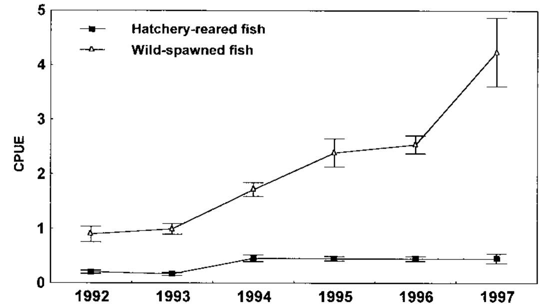

FIGURE 4.—Mean (±SE) total electrofishing catch (CPUE = catch per minute) of stocked (hatchery-reared) and wild-spawned rainbow trout from 1992 to 1997 in the Lee's Ferry tailwater, Colorado River.

ever, we incorporated them into our analyses to evaluate possible differences in rainbow trout spatial distributions and trends in the tailwater. Relative condition factor ($K_n = W/W'$) was calculated for trout 100 mm and larger, where W = total wet weight (g), $W' = 10^{-4.6 + 2.856\log_{10}L}$, and L = TL. The length-specific mean-weight equation used in this study (W') was developed for Lee's Ferry rainbow trout collected in the tailwater during 1984–1990 using the 75th-percentile technique (Murphy et al. 1990, 1991).

Data for catch rates were kurtotic and therefore were log-transformed. Because dam discharge data were nonnormally distributed, we used rank correlations, not to test hypotheses but to identify possible relationships between dam operation (mean, minimum, coefficient of diel variation [CV; SD/mean], and total hours at water releases of 227 m^3/s or less), catch per unit effort (CPUE), and K_n of rainbow trout. We evaluated total hours of flows at 227 m^3/s or less because discharges below this level have resulted in high proportional losses of wetted perimeter of the river channel, reduced available benthic prey, and potentially influenced trout production in the tailwater (Blinn et al. 1995; Benenati et al. 1998).

Results

Catch per Minute

Year ($F = 42.8$, df = 6, $P \leq 0.0001$) and sampling location ($F \geq 9.2$, df = 14, $P \leq 0.0001$) were significant main effects on catch per minute for all rainbow trout combined. Interaction between location and year was not significant ($F = 0.9$, df = 78, $P = 0.7770$) and length-specific catch rates differed among years (Figure 3). Effects of year on catch per minute were significant for all length categories of trout ($F \geq 21.3$, df = 6, $P \leq 0.0001$); CPUE was lowest during 1991–1993 and greatest in 1997 for small trout. Catch rates for large trout 305–405 mm declined from 1991 to 1993 and then increased through 1997. Catch rates of trout 406–558 mm were highest in 1991 and declined to essentially stable levels between 1994 and 1997 ($F \geq 39.1$, df = 6, $P \leq 0.0001$; Figure 3). Analyses of catch rates in 50-mm increments indicated stockpiling of smaller trout near the lower limits of the slot (percentages of total catch within the slot: 400–449 mm, 9.4%; 450–499 mm, 3.5%; 500–550 mm, 0.6%).

Catch rates of both stocked and wild-spawned rainbow trout also differed significantly among years ($F \geq 10.8$, df = 5, $P \leq 0.0001$) and sampling locations ($F \geq 3.6$, df = 14, $P \leq 0.0002$); interaction was not significant ($F \geq 0.8$, df = 64, $P \geq 0.2303$). Catch per minute of stocked trout nearly doubled and stabilized after 1993, whereas CPUE of wild-spawned trout increased between 1993 and 1997 (Figure 4).

Catch per minute of small rainbow trout and trout 305–405 mm were positively correlated ($r \geq 0.5138$, $N = 23$, $P \leq 0.0121$) with mean daily flows. Though catch rates of small trout were negatively correlated with mean CV and with total hours monthly for releases up to 227 m^3/s from the dam ($r \geq -0.4825$, $N = 19–20$, $P \leq 0.0364$), CPUE for large trout was independent of flow-variability indices ($P \geq 0.05$).

Relative Condition Factor

Year ($F = 35.1$, df = 6, $P \leq 0.0001$) and sampling location ($F = 7.5$, df = 14, $P \leq 0.0001$) were significant main effects on relative condition of all trout combined; interaction between location and year was not significant ($F = 0.9$, df = 78, $P \leq 0.6107$). Relative condition declined for all trout

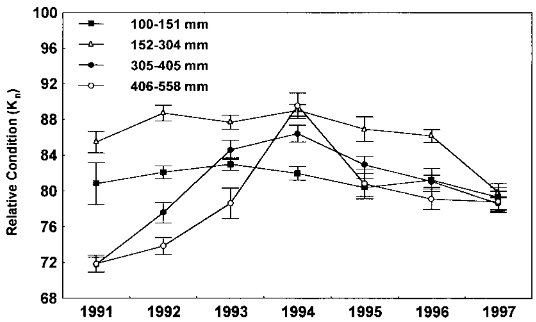

FIGURE 5.—Mean (±SE) relative condition (K_n) of rainbow trout of different lengths caught by electrofishing from 1991 to 1997 in the Lee's Ferry tailwater, Colorado River.

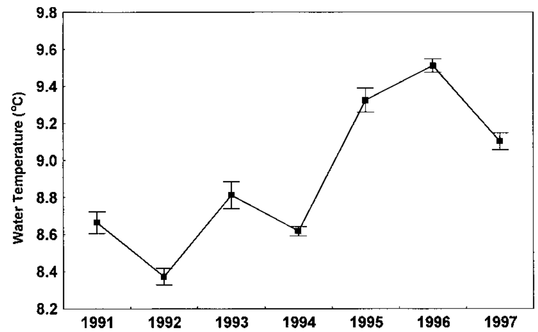

FIGURE 6.—Mean (±SE) water temperature of discharge at Glen Canyon Dam into the Lee's Ferry tailwater, Colorado River, 1991–1997.

combined between 1994 and 1997. Year ($F \geq 10.7$, df $= 5$, $P < 0.0001$) and sampling location ($F = 3.6$, df $= 14$, $P < 0.0005$) were significant main effects on the relative condition of both stocked and wild-spawned trout, and interaction was not significant ($F \leq 1.2$, df $= 64$, $P < 0.2303$). Relative condition also varied among years for different length-classes, but tended to become more uniform over time (Figure 5). Condition of trout less than 151 mm did not differ significantly among years ($F = 1.0$, df $= 6$, $P \leq 0.4378$), but condition of trout 152–304 mm declined nearly 8% in 1997 ($F = 12.1$, df $= 6$, $P \leq 0.0001$). Condition of large trout improved between 1991 and 1994, then declined about 10% by 1997 ($F = 21.0$, df $= 6$, $P \leq 0.0001$).

The relative condition of small rainbow trout was negatively correlated with mean daily discharge ($r \geq -0.4219$, $N = 23$, $P \leq 0.0449$), whereas the condition of large trout 406–558 mm was negatively correlated with mean CV of dam releases ($r \geq -0.5018$, $N = 19$, $P = 0.0286$). Within size categories, CPUE and condition were negatively correlated only for trout 305–405 mm ($r = -0.4585$, $N = 23$, $P = 0.0278$).

Water Temperature

Mean temperatures of dam discharges into the Lee's Ferry tailwater differed among years ($F = 39.6$, df $= 6$, $P < 0.0001$), ranging between 8.4°C and 9.6°C during the study. Water temperatures were warmer from 1995 to 1997 than in other years (Figure 6). For releases up to 227 m^3/s from the dam, water temperature was positively correlated with mean flow and negatively correlated with mean CV and total hours ($r \geq -0.4429$, $N = 23$–28, $P \leq 0.0444$). Catch rates were positively correlated with mean water temperatures only for small trout ($r \geq 0.4585$, $N = 23$, $P \leq 0.0278$).

Angling and Stocking

Annual stocking of fingerling rainbow trout (≤120 mm TL) declined from 72,000 fish in 1991 to 25,000 in 1997, yet angler catch rates of rainbow trout doubled between 1991 and 1997 (Table 1). Angler use declined between 1991 and 1993 and then increased through 1997 (Table 1). Total angling harvest declined after 1991 and stabilized at about 4,000 fish/year by 1994 (Table 1). Angler catch rates were positively correlated with electrofishing catch rates for all trout ($r = 0.9286$, $N = 7$, $P = 0.0025$), but not with stocking rates for trout ($r = -0.3214$, $N = 7$, $P = 0.4821$). Stocking rates also were not correlated with electrofishing catch rates, relative condition, or harvest ($r \leq 0.5585$, $N = 7$, $P \geq 0.1754$).

Discussion

Our results generally support previous conclusions that alterations in flow regimes in regulated rivers influence fish populations (Weisberg and

TABLE 1.—Annual stocking (number of fish ≤ 120 mm total length), angler catch (fish/h for each angler), use (1,000 × angler-hours/year), and harvest (fish creeled/year) of rainbow trout in the Lee's Ferry tailwater, 1991–1997.

Year	Fish stocked	Angler catch	Angler use	Angler harvest
1991	72,000	0.56	242.4	10,076
1992	78,000	0.41	110.4	3,216
1993	73,000	0.49	55.4	2,051
1994	103,000	0.74	79.5	4,157
1995	73,000	0.88	100.1	4,005
1996	20,000	1.11	132.8	5,311
1997	25,000	1.10	177.9	4,000

Burton 1993; Travnichek et al. 1995; Bowen et al. 1998). Before mid-1991, diel releases from Glen Canyon Dam fluctuated widely, mean daily flows were highly variable, and minimum flows often reached about 85 m^3/s (Patten 1991; U.S. Department of Interior 1995). However, minimum daily releases from the dam increased to 142 m^3/s after 1991, and mean daily fluctuations in flows stabilized.

The stabilized flow regime after 1991 helped support increased relative abundance and survival of rainbow trout and also increased angler catches. Interpretation of our results is weakened somewhat by the lack of electrofishing data before inception of the stabilized flow regime. However, our conclusion is supported by trends in angler catch rates, which increased from 0.13−0.80 fish$\cdot h^{-1} \cdot d^{-1}$ between 1980 and 1990 (McKinney and Persons 1999) to 0.88–1.11 fish$\cdot h^{-1} \cdot d^{-1}$ between 1995 and 1997. Higher releases from the dam may be associated with lower electrofishing catch rates (McKinney et al. 1999b, 1999c); however, the electrofishing catch rate increased after 1994, despite a doubling of mean daily releases from the dam. Thus, we suggest that our results and conclusions were minimally influenced by any changes in electrofishing efficiency associated with dam releases at the times of sampling.

The relative abundance of both stocked and wild-spawned rainbow trout increased following stabilized releases from the dam, but an upward trend was evident only for wild-spawned trout. Although spatial distribution within the Lee's Ferry reach influenced electrofishing catch rates and relative condition, within-site changes in these variables were comparable among years and indicated changes in the relative abundance of rainbow trout throughout the dam tailwater. Weisberg and Burton (1993) found that growth and condition of three fish species were greater following inception of a minimum-flow requirement for a hydroelectric dam. Travnichek et al. (1995) also reported a twofold increase in species richness and a fivefold increase in numbers of warmwater fishes in a dam tailwater following increased minimum water releases and reduced fluctuations in flow.

We infer that dam operation is a primary driving variable that influences the rainbow trout population in the Lee's Ferry tailwater. However, McKinney et al. (1999b, 1999c) found that isolated flow-related disturbances of moderate magnitude and duration had little influence on rainbow trout population indices in the Lee's Ferry reach, even though the aquatic food base was reduced in association with the events. Furthermore, rainbow trout stocking rates were not significantly associated with electrofishing catch rates, relative condition, angler catch rates, or harvest, suggesting that stocking had little influence on the fishery. In contrast, the relative abundance and condition of flannelmouth sucker in the tailwater were essentially unchanged during stabilized flows (McKinney et al. 1999a), suggesting differential influences of the modified releases on native and nonnative fishes in the tailwater.

The greater relative abundance of rainbow trout in the Lee's Ferry tailwater probably corresponded with a more extensive food base associated with reduced fluctuations in discharge from the dam (Angradi and Kubly 1993; Blinn et al. 1995; Benenati et al. 1998) as well as with warmer mean water temperatures between 1995 and 1997. In contrast, the decline in the relative condition of trout suggests a negative association between relative abundance and the condition of trout in the tailwater.

Our results further indicated that the changes in relative abundance and condition associated with dam operation were length specific: small rainbow trout in the Lee's Ferry tailwater were more responsive to physical habitat conditions than large trout. Our results are supported by Schlosser (1985), who suggested that the abundance of younger age-classes of fish may be influenced more by physical factors, such as temperature and water level, whereas the abundance of older age-classes may be regulated more by biotic interactions. Walters and Post (1993) also predicted that if small and large fish have different habitat preferences, increases in densities will affect large fish more than small fish.

Suitable habitat is a key variable that influences fishes in coldwater streams (Binns and Eiserman 1979; Orth and Maughan 1982; Griffith 1993). We provide empirical evidence that stabilized flow regimes provide conditions that support greater relative abundance of rainbow trout. This may be possible, in part, because of greater continuous availability of shallow, nearshore areas (Bain et al. 1988; Scheidegger and Bain 1995; Bowen et al. 1998) and a more extensive food base (Blinn et al. 1995; Benenati et al. 1998). Our results support the conclusion that frequent and large fluctuations in discharge from hydroelectric power dams impair the stability and quality of shallow, nearshore habitats (Bain et al. 1988; Blinn et al. 1995; Bowen et al. 1998) and negatively influence the relative abundance of small rainbow trout.

Our results also suggest that the warmer nearshore areas necessary for refuge and nurseries develop during more stable flows. Near-optimal water temperatures (to about 20°C) have been recorded in nearshore and backwater nursery areas during high, steady releases (about 625 m^3/s) from Glen Canyon Dam, when main-channel temperatures were about 9–10°C (AGFD, unpublished data). Increased relative abundance of small rainbow trout also was positively associated with higher water temperature in our study, suggesting beneficial effects of warmer water (Filbert and Hawkins 1995; Childs et al. 1998) on juvenile fish (Hokanson et al. 1977). Small fish tend to inhabit shallow, nearshore zones and do not move into deeper, mid-channel water until they increase in size (Griffith 1993; Walters and Post 1993; Scheidegger and Bain 1995). As stream size increases, large concentrations of small fish may become increasingly restricted to stream margins, while deeper areas are inhabited primarily by larger, older fish (Schlosser 1985; Bain et al. 1988; Bowen et al. 1998). If unstable shallow-water habitats provide less-effective refuge areas for small fish, densities will decline (Bain et al. 1988; Scheidegger and Bain 1995; Bowen et al. 1998).

Conclusions

Managing dams to improve or maintain riverine populations of rainbow trout requires understanding the responses of both fish and the aquatic food base to flows (Blinn et al. 1995; Stevens et al. 1997). We demonstrated changes in relative abundance and condition of rainbow trout following implementation of a stabilized flow regime, but we were unable to develop truly controlled, replicable studies. Regardless, we believe our results contribute to the understanding of rainbow trout ecology in a regulated river. Our results indicate that a stabilized flow regime benefited the rainbow trout recreational fishery below Glen Canyon Dam, as measured by increases in the relative abundance of trout, angler success, and use of the resource. Managers also may need to consider a trade-off between producing large numbers or large sizes of rainbow trout in the Lee's Ferry tailwater (Walters and Post 1993; Bohlin et al. 1994). High densities of fish often correspond with declines in survival, growth, size, and condition (Medland and Beamish 1985; Elliott 1987; Walters and Post 1993), which may be mediated to some degree by declines in the food base (Weiland and Hayward 1997). Above some level of rainbow trout densities or fishing pressure, the ''quality'' aspects of a fishery may be sacrificed because larger, older fish exist in greatly reduced numbers (Anderson and Nehring 1984; Bohlin et al. 1994).

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