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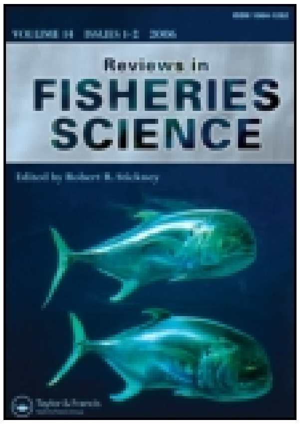

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Novel Fish Communities: Native and Non-Native Species Trends in Two Run-of-the-River Reservoirs, Clark Fork River, Montana

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Long-term (1955–2011) trends in fish community structure were investigated in Noxon and Cabinet Gorge Reservoirs, Montana, based on the analysis of gillnet catches since the construction of the reservoirs. Results of gillnetting show significant declines in several forage species in absolute and relative abundance since the mid-1990s. Catches have declined for forage species as a group and for individual species such as non-native yellow perch Perca flavescens, native suckers Catostomus spp.*, and native peamouth Mylocheilus caurinus. In contrast, the aggregate catches of the non-native predators increased greatly as a percentage of the total catch since the 1990s, including increases in catches of walleye Sander vitreus, and northern pike Esox lucius. As a result of the non-native species increases, species diversity has, overall, trended upward whereas species dominance based on the three most abundant species has decreased, as previously abundant forage species have been reduced and greater evenness has resulted. Overall, the fish community in the reservoirs has shifted from a natural, seasonally coldwater riverine system (pre-impoundment) to a modified, coldwater-managed (i.e., salmonid stocked) system in the 1950s through the 1970s to a coolwater system dominated by forage species in the 1980s and early to mid-1990s, and, most recently, to a coolwater system more strongly structured by non-native piscivores. This novel (i.e., native-non-native) community poses some difficult issues for managers on which species to proactively manage for. Additional effort is needed to assess benefits and costs of proactively managing for non-natives as part of successful, comprehensive management plans.*

Keywords reservoir fishery management, non-native fish, walleye, Montana, Clark Fork River, novel ecosystems

Fish faunas across the continental United States have become more similar through time because of widespread introductions of a group of species intended to enhance food and sport fisheries... Introduction of [fish] species outside their native range continues to be a major problem in the United States...” (Rahel, 2000, pp. 854, 856).

“While intentional and unintentional introductions of non-native species have accounted for ...[their] initial establishment ..., *habitat change* is currently the major factor causing the[ir] expanded distribution and increasing abundance ... in the Columbia River Basin. Most of the free-flowing river habitats in the Snake and Columbia Rivers have been converted into reservoir habitats through dam building... The reservoirs have created hotspots of non-native species, which become source populations of non-natives, facilitating secondary spread of these species throughout the basin” (Independent Scientific Advisory Board, 2008, p. iii).

...“we predict the proportion of non-native species that are [sic] viewed as benign or even desirable will slowly increase over time as their potential contributions to society and to achieving conservation objectives become well recognized and realized” (Schlaepfer et al., 2011, p. 428).

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> "It is obvious that if there remains any hope for the survival of folk music in the near or distant future (a rather doubtful outcome considering the rapid intrusion of higher civilization into the more remote parts of the world), an artificial erection of . . . walls to separate peoples from each other bodes no good for its development. A complete separation from foreign influences means stagnation: well assimilated foreign impulses offer possibilities of enrichment" (Béla Bartók, 1942; in Suchoff, 1976, p. 31).

INTRODUCTION

Reservoir construction for flood control, hydropower, municipal and industrial use, and agriculture has coincided with rapid changes of many freshwater fish communities and fisheries in regulated rivers (Bain et al., 1988; Bonner and Wilde, 2000) and reservoirs. Habitat changes combined with introductions of non-native prey and predator species, intentionally, accidentally, or surreptitiously (i.e., illegally), have resulted in unprecedented hybrid and novel fish communities. Hybrid systems can be viewed as those modified in abiotic and biotic characteristics, species composition and function, whereas novel systems are those potentially irreversibly changed in those characteristics (Hobbs et al., 2006, 2009). More lentic and fewer lotic habitats inhabited by introduced species have resulted in altered food webs (Independent Scientific Advisory Board, 2011; Naiman et al., 2012) and new fisheries (McMahon and Bennett, 1996). These newly constituted reservoir fish communities and the fisheries on them pose entirely new management problems (Miranda, 1996; Hobbs et al., 2006; Independent Scientific Advisory Board, 2008; Sanderson et al., 2009).

One example of issues involving novel fish communities in reservoirs is the case of Cabinet Gorge Reservoir (hereafter CGR; completed 1953) and adjacent Noxon Reservoir (hereafter Noxon; completed 1959), two mainstem hydroelectric impoundments on the Clark Fork River in western Montana (Huston, 1985; Figure 1). Prior to the construction of Thompson Falls Dam in 1913 and Cabinet Gorge and Noxon Rapids dams decades later, the mainstem Clark Fork River served as a continuous migratory corridor and rearing area for native riverine species, including adfluvial bull trout *Salvelinus confluentus* and other fish migrating up from Lake Pend Oreille in Idaho (Huston, 1988). Soon after Cabinet Gorge and Noxon reservoirs filled, fisheries investigations and management actions began in an attempt to improve fisheries, including a pre-Noxon Dam fish eradication many subsequent stockings of salmonids (summarized in Huston, 1985; Liermann and Tholl, 2003, and Horn and Tholl, 2010). Throughout the existence of the reservoirs, many species, habitat and operational changes have occurred. The native bull trout has been greatly depleted throughout much of its interior range, including the Clark Fork system and is listed as a threatened species under the Endangered Species Act (U.S. Fish and Wildlife Service, 1999). Construction of the three dams probably aided in this decline. In addition, there has been a periodic addition of non-native fish species (e.g., northern pike *Esox lucius*, basses *Micropterus* spp., and walleye *Sander vitreus*) and other organisms introduced during the more than half century of reservoir existence. Fisheries management under such conditions presents major challenges as species interactions and angler preferences exist in a state of continual, rapid change.

Efforts at monitoring the fish community through gillnet sampling with similar, and more recently (2000), completely standardized, nets have resulted in a long-term data base extending from 2011 as far back as 1955 for CGR and 1959 for Noxon, although data are unavailable for some intervening years. Although any such datasets have some limitations because of the inherent species selectivity of gillnets or any one gear (Hubert, 1996), the Noxon and CGR datasets remain useful for tracking long-term changes in the fish community and the accompanying management problems.

Our objectives are to (1) characterize the fish species community characteristics and trends for the two reservoirs over the past half-century based on the gillnet sampling data and (2) identify and evaluate key factors influencing the trends, including management activities and introductions of non-native species.

STUDY SITE

Both CGR and Noxon are run-of-the-river hydroelectric impoundments. With the completion of Cabinet Gorge Dam, just inside the Idaho state line, in 1953, CGR (which lies mostly within Montana) was 32-km long with an average width of 0.6 km. Maximum pool area is 1,417 Ha. Details of the dam and catchment can be found at http://npdp.stanford.edu/DamDirectory/DamDetail.jsp?npdp_id=ID00222.

With the completion of Noxon Rapids Dam upriver of CGR, filling of Noxon Reservoir occurred from August 1958 through the summer of 1959. Its surface area is 3,583 Ha at full pool. Details of the dam and catchment area can be found at http://npdp.stanford.edu/DamDirectory/DamDetail.jsp?npdp_id=MT00223. As of 2012, no upstream fish passage is provided at either of the two dams. However, adult bull trout passage upriver past Cabinet Gorge Dam using capture and haul methods began in 2001.

Huston (1985) and Liermann and Tholl (2003) summarized limnological conditions of the reservoirs. Water exchange rates for both reservoirs are high; for CGR about one week during average inflow and 1–2 days during high water. CGR can primarily be characterized as riverine (Liermann and Tholl, 2003). For Noxon, water exchange rates are lower, about three weeks during average inflow and about one week during high water. Noxon consists of two distinct habitat types that were identified for sampling as two distinct strata. The lower Noxon Stratum from Beaver Creek Bay down-reservoir to the dam, a distance of about 32 km (hereafter NS1) is standing water except for during high-flow periods or severe reservoir drafting. NS1 has

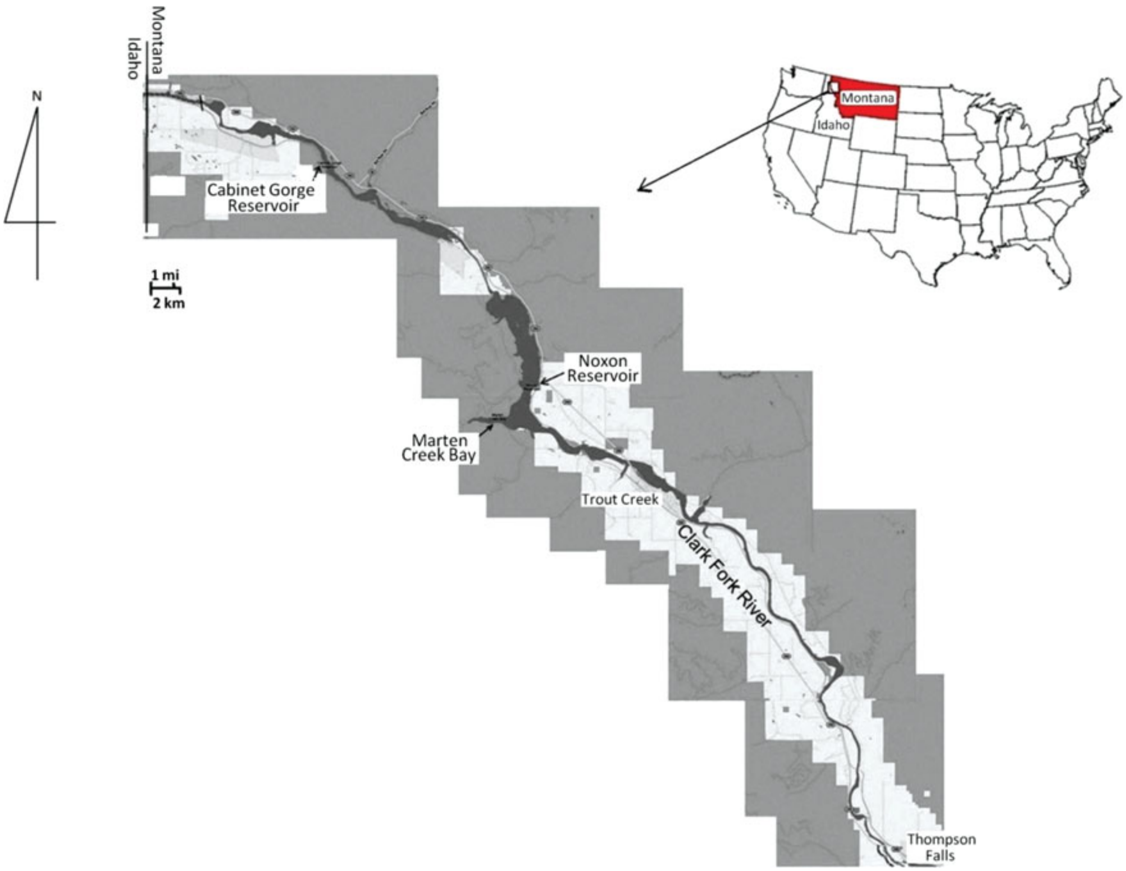

Figure 1 Noxon and Cabinet Gorge Reservoirs, Montana.

an extensive littoral zone and is about 1.2 km wide. The upper Noxon Stratum from and including Beaver Creek Bay to Thompson Falls Dam (hereafter NS2) has a U-shaped channel and noticeable current at most times of the year.

The two reservoirs differ in their seasonal temperature profiles. Huston (1985) reported that CGR was almost always isothermal because of its control by Noxon Rapids Dam and its rapid exchange rate. In contrast, although Noxon does not typically form a thermocline, it does show substantial variation of summer water temperature by depth, ranging from 20°C or slightly higher at the surface to 10°C at depths of 50 m or more. Inflowing rivers and streams provide thermal refuges for cold water fish species during summer.

Significant changes in hydroelectric operations have occurred since the creation of the two reservoirs. In particular, reservoir-operations decisions have greatly affected water drawdowns in both reservoirs (Liermann and Tholl, 2003). For CGR from 1952 to 1985, no restrictions were placed on reservoir levels, even though the penstock depth (4.6 m) limited the drawdown. However, from 1985 through 1999, the 4.6-m annual fluctuations were eliminated and a 1.3-m maximum (and daily) drawdown adopted. The maximum allowable drawdown was increased to 2.3 m in 1999 to meet minimum flow requirements for the Clark Fork River below the dam. In Noxon, from 1958 to 1960, drawdowns averaged about 0.3 m per day and ranged from 1.0 to 1.6 m per week. From 1961 to 1978, annual maximum drawdowns ranged from 9 to 18 m; no water level restrictions were in place on Noxon, and annual drawdowns of 10 m or more were common. In 1979, a voluntary operation change was implemented, with winter drawdown reduced significantly. This change was formalized in 1985, when the annual maximum drawdown was limited to 3 m, in increments not to exceed 0.6 m per day. Starting in 1999, the maximum drawdown was 1.3 m from May 15 through September 30, with maximum daily drawdowns of 0.6 m. The stabilization of water levels was designed to improve habitat conditions and thus the survival of basses and other fish species.

The fish community in CGR and Noxon consists of a mixture of at least 23 coldwater and warmwater species (Horn and Tholl, 2010). Non-native fish species that are relatively abundant and provide the majority of recreational angling include largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, northern pike, and yellow perch *Perca flavescens*. Other non-native species are walleye, lake whitefish *Coregonus clupeaformis*, lake trout *Salvelinus namaycush*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, pumpkinseed *Lepomis gibbosus*, black bullhead *Ameiurus melas*, yellow bullhead *Ameiurus natalis*, and occasional kokanee *Oncorhynchus nerka*. Rainbow trout *Oncorhynchus mykiss* have also been heavily stocked in the past and remain common. Native non-game species currently found include northern pikeminnow *Ptychocheilus oregonensis*, peamouth *Mylocheilus caurinus*, redside shiners *Richardsonius balteatus*, largescale suckers *Catostomus macrocheilus*, and longnose suckers *Catostomus catostomus*. Due to warm summer water temperatures contributed by the lower Flathead River, the lower Clark Fork River before impoundment was more of a migratory corridor than year-long rearing habitat for native salmonids. Fish eradication efforts with rotenone in the 1960s further reduced native salmonids (Huston, 1985). However, populations of native bull trout, westslope cutthroat trout *Oncorhynchus clarki lewisi*, and mountain whitefish *Prosopium williamsoni* have persisted in tributaries and the reservoirs since then. These native species were always less abundant in the reservoirs than warmwater and coolwater water species in the lower Clark Fork and reservoirs (Huston, 1985), and have been sampled infrequently at the gill net sites used since 2000. Northern pike, thought to have entered the Clark Fork from the Little Bitterroot River through an illegal stocking in Lonepine Reservoir in the late 1950s (Horn and Tholl, 2010), were first captured in Noxon in 1972, in CGR in 1974, and in Lake Pend Oreille in 1975. In 1982 smallmouth bass were experimentally stocked in Noxon for sport fishery potential. In 1984 they were observed in both reservoirs in substantial numbers. Both smallmouth bass and largemouth bass were stocked periodically from the mid-1980s through mid-1990s. As of 2012, both species are established in the reservoirs and support numerous annual fishing tournaments. Walleye, another unofficial introduction, have also been found (Horn and Tholl, 2010); recent sampling of young walleye in both CGR and Noxon strongly suggests that the species is now self-sustaining (Avista Utilities, 2011, Unpublished data).

METHODS

Data from gillnet catches were analyzed in terms of three strata: CGR, Noxon Stratum 1 (NS1; lower portion of reservoir), and Noxon Stratum 2 (NS2; upper portion of reservoir). Samples were collected from 1955 through 2011 in CGR and 1959 through 2011 in Noxon. From 2000 to 2011, all data were collected using completely standardized gillnets. The standard survey consisted of 45 gillnets set in October at standard locations throughout the reservoirs. These nets were 38 m long and 1.8 m deep with five 7.6-m panels with bar mesh of 1.9 cm, 2.5 cm, 3.2 cm, 3.8 cm, and 5.1 cm (Horn and Tholl, 2010). Gillnets were set in the afternoon and fished for approximately 18 hr overnight. Except for open-water sets, the nets were set mostly near the bottom and perpendicular to shore, with the smallest mesh toward shore. Data collected before 2000 were not completely standardized with later years. Sampling in the 1990s and before occurred in other months besides October (Washington Water Power, 1996a,b) and included more and different gill net sites. In the 2000s, after bull trout listing, early October sampling was designed to reduce trout mortalities; bull trout would typically be up tributaries and brown trout would typically be staging by tributary mouths in preparation for spawning.

Upon retrieval, nets were brought to shore and fish were removed for processing. Data collected from each fish included species, total length, and weight. All data were linked to a particular net and site. Additional details of the sampling since 2000 are described in Horn and Tholl (2010).

Although standardized gillnet data (catch per standard net over a standard time period) would ideally be used for all years, data prior to 2000 were collected in situations where net length and mesh sizes or combinations of meshes employed were often not adequately described. In addition, aggregate catches were often grouped among two or more nets. Duration of set was often not recorded. For these reasons, we were unable to find an entirely satisfactory way to standardize catches. Because nets used prior to 2000 were in general similar to those used starting in 2000, our approach was to calculate mean catch per net for the five or more nets used each year (i.e., however many nets were set as long as it was five or more) and use that mean catch per net as an index of relative abundance to compare with data starting in 2000. We assumed that because of natural variation in catches, the minimum of five or more gillnets was necessary for monitoring fisheries at each stratum. This approach resulted in a few additional years with missing data. For example, catches for NS2 in 1959 were not used because only three gillnets were set that year (Table 1). Number of gillnets set, number of aggregate fish captured (i.e., combining individuals of all observed fish species), and corresponding mean number of fish per net (or combined catch for all species) for three sites over observed years are provided in Table 1.

Fish community and individual species analyses – For species in aggregate and individual species, relative abundance indices expressed as the natural log (base e) of mean number of fish per net (MNFPN) were calculated, data permitting, for each year from 1955 in CGR and from 1959 in NS1 and NS2. Scatter plots of each species log-MNFPN versus year were made and associated linear regressions were also calculated. Log-transformed data were used to better meet regression assumptions. Linear regression of log-MNFPN for aggregate species was performed for each site using two time periods: (1) years before 1994 and (2) those from 1994 to 2011. The period beginning 1994 was based on observations of scatter plots of the moving average of total aggregate log fish catches, which tended to show a change of trends in numbers of fish in NS1, NS2, and CGR prior to and after the year 1994.

Individual species trends were also analyzed with regression analysis of mean log MNFPN as the y-variate and time as the x-variate. Various time periods were used for quantifying trends depending on data available and results of preliminary scatter plots.

Fish community analyses – For a community-level assessment, selected species were grouped and subjected to trend analyses. The first approach used was to create three groups

Table 1 Available years of gillnet data from Noxon Stratum 1 (NS1) and Noxon Stratum 2 (NS2), 1959–2011, and Cabinet Gorge Reservoir (CGR; 1955–2011), number of nets (Nets), total fish captured (No. of fish), and mean number of fish per net (MNFPN)

	Site								
	NS1			NS2			CGR		
Year	Nets	No. of fish	MNFPN	Nets	No. of fish	MNFPN	Nets	No. of fish	MNFPN
1955*	·	·	·	·	·	·	**16**	**927**	**57.94**
1956*	·	·	·	·	·	·	·	·	·
1957*	·	·	·	·	·	·	·	·	·
1958*	·	·	·	·	·	·	**13**	**169**	**13.00**
1959	**9**	**152**	**16.89**	3	99	33.00	**17**	**640**	**37.65**
1960	**28**	**985**	**35.18**	**7**	**137**	**19.57**	**30**	**1011**	**33.70**
1961	**51**	**1297**	**25.43**	**21**	**252**	**12.00**	**22**	**438**	**19.91**
1962	**33**	**1552**	**47.03**	**7**	**306**	**43.71**	**50**	**762**	**15.24**
1963	**36**	**1308**	**36.33**	**6**	**100**	**16.67**	**19**	**417**	**21.95**
1964	**40**	**1059**	**26.48**	**18**	**437**	**24.28**	**41**	**1212**	**29.56**
1965	**30**	**1723**	**57.43**	**16**	**347**	**21.69**	**17**	**885**	**52.06**
1966*	4	643	160.75	·	·	·	**6**	**245**	**40.83**
1967	**8**	**260**	**32.50**	3	29	9.67	4	57	14.25
1968*	·	·	·	·	·	·	·	·	·
1969	**43**	**1672**	**38.88**	**13**	**257**	**19.77**	**17**	**548**	**32.24**
1970*	·	·	·	·	·	·	·	·	·
1971*	·	·	·	·	·	·	·	·	·
1972*	·	·	·	**5**	**61**	**12.20**	**6**	**103**	**17.17**
1973*	·	·	·	·	·	·	·	·	·
1974*	·	·	·	·	·	·	**12**	**384**	**32.00**
1975*	·	·	·	·	·	·	·	·	·
1976	**74**	**1741**	**23.53**	4	485	121.25	**10**	**109**	**10.90**
1977*	·	·	·	·	·	·	·	·	·
1978*	·	·	·	·	·	·	·	·	·
1979	**5**	**292**	**58.40**	·	·	·	**5**	**97**	**19.40**
1980	**20**	**2080**	**104.00**	·	·	·	**8**	**530**	**66.25**
1981*	·	·	·	·	·	·	·	·	·
1982	**23**	**736**	**32.00**	3	123	41.00	**14**	**384**	**27.43**
1983*	·	·	·	·	·	·	·	·	·
1984*	·	·	·	·	·	·	·	·	·
1985*	·	·	·	·	·	·	·	·	·
1986	**18**	**772**	**42.89**	1	25	25.00	**6**	**203**	**33.83**
1987	**43**	**2004**	**46.61**	**12**	**394**	**32.83**	**7**	**284**	**40.57**
1988	**38**	**3127**	**82.29**	**8**	**208**	**26.00**	4	99	24.75
1989	**30**	**1878**	**62.60**	·	·	·	**20**	**375**	**18.75**
1990	**39**	**1438**	**36.87**	**6**	**102**	**17.00**	**19**	**285**	**15.00**
1991	**21**	**1111**	**52.91**	**12**	**240**	**20.00**	·	·	·
1992	**15**	**508**	**33.87**	1	188	188.00	**22**	**584**	**26.55**
1993	**30**	**2470**	**82.33**	**5**	**222**	**44.40**	**11**	**247**	**22.46**
1994	**18**	**2464**	**136.89**	2	458	229.00	**15**	**661**	**44.07**
1995	**10**	**711**	**71.10**	2	113	56.50	**6**	**107**	**17.83**
1996*	·	·	·	·	·	·	·	·	·
1997	**20**	**766**	**38.30**	·	·	·	·	·	·
1998*	·	·	·	·	·	·	·	·	·
1999*	·	·	·	·	·	·	·	·	·
2000	**18**	**1068**	**59.33**	**11**	**398**	**36.18**	**15**	**333**	**22.20**
2001*	·	·	·	·	·	·	·	·	·
2002	**19**	**912**	**48.00**	**11**	**461**	**41.91**	**15**	**298**	**19.87**
2003	**19**	**885**	**46.58**	**11**	**388**	**35.27**	**15**	**340**	**22.67**
2004	**19**	**596**	**31.37**	**11**	**260**	**23.64**	·	·	·
2005	**19**	**759**	**39.95**	**11**	**241**	**21.91**	**15**	**240**	**16.00**
2006	**19**	**869**	**45.74**	**11**	**330**	**30.00**	**15**	**271**	**18.07**
2007	**19**	**611**	**32.16**	**11**	**348**	**31.64**	**15**	**197**	**13.13**
2008	**19**	**554**	**29.16**	**11**	**172**	**15.64**	**15**	**165**	**11.00**
2009*	·	·	·	·	·	·	·	·	·
2010	**19**	**762**	**40.11**	**11**	**252**	**22.91**	**15**	**290**	**19.33**
2011	**19**	**593**	**31.21**	**11**	**209**	**19.00**	**15**	**165**	**11.00**

An asterisk (*) indicates years with no gill net data or less-than-five gill nets used. Data in bold met criteria for minimum number of nets to be used in analysis.

of fish (Forage, Non-native Predator, and Trout). The Forage Group consisted of largescale sucker, longnose sucker, redside shiner, peamouth, pumpkinseed, and yellow perch. The Non-native Predator Group consisted of northern pike, walleye, largemouth bass, and smallmouth bass. The Trout Group consisted of bull trout, brown trout, brook trout, cutthroat trout (Yellowstone and westslope), lake trout, and rainbow trout. Log-MNFPN values for the three groups were examined for trends. Log-MNFPN for each group was obtained by combining Log-MNFPN of each species included in the group. Also, percentages of each group in total catches over observed years were examined. Scatter plots and linear regressions of log-MNFPN against year were used for each group. We hypothesized that the Forage Group would trend over time inversely with the Non-native Predator group.

Fish community attributes were also characterized according to richness and relative abundance (evenness). Simpson's diversity index (SDI) was used (Washington, 1984). SDI is based on Simpson's measure of concentration or $D = \sum(p_i)^2$ where p_i = proportion of ith species in a sample, and $i = 1,2,\ldots,s$ (s is the number of species in a sample.). Simpson's D measures the probability that two individuals randomly selected from a sample will belong to the same species. D is also considered a dominance index because it weights toward the abundance of the most common species. D was expressed as:

$$D = [\Sigma n_i(n_i - 1)]/[N(N - 1)],$$

where n_i = number of ith species fish in a sample, $i = 1, 2,\ldots, s$ (s is the number of species in a sample), and N = total number of fish of all species in a sample or $\sum n_i$. D ranges between 0 and 1; the larger the value of D, the lower the diversity. Subtracting D from 1 gives SDI:

$$\text{SDI} = 1 - D = 1 - \left\{\left[\Sigma n_i(n_i - 1)\right]/\left[N(N - 1)\right]\right\}.$$

SDI also ranges between 0 and 1, but the greater the value of SDI, the greater the sample diversity. SDI represents the probability that two individuals randomly selected from a sample will belong to different species.

The expression for the variance (s^2) of SDI is:

$$s^2 = 4\left[\Sigma p_i^3 - \left(\Sigma p_i^2\right)^2\right]/N,$$

where $p_i = n_i/N$, n_i = number of individuals in species i, and N = total number of individuals for all species in fish assemblage.

We used a t-test to determine whether SDI values were different or not for fish assemblages from two sites (e.g., 1 and 2). We first calculated a t-statistic (t_{obs}):

$$t_{\text{obs}} = |\text{SDI}_1 - \text{SDI}_2|/\left[\text{SQRT}\left(s_1^2 + s_2^2\right)\right],$$

where SDI_1 and SDI_2 are SDI obtained from Site 1 and 2, respectively, $s_1{}^2$ and $s_2{}^2$ are variance of SDI_1 and SDI_2, respectively, and SQRT is the square root function. The value of t_{obs} was then compared to a critical t-value which is $t[\alpha/2,\text{df} = (\text{number-of-species-Site-1}) + (\text{number-of-species-Site-2}) - 2]$ from a t-test table. If $t_{\text{obs}} > t(\alpha/2,\text{df})$, then the difference between two sites was considered to be significant. If not, then no difference was found between the two sites.

Because reporting only diversity as an assemblage structural index does not adequately consider the effects of species richness and evenness, we also calculated a corresponding index of evenness. The Evenness index for SDI (ESDI or V') was calculated as

$$\text{ESDI or } V' = (1 - D)/(1 - D)_{\max} = (1 - D)/[1 - (1/s)],$$

where $(1 - D)_{\max} = [1 - (1/s)]$ = possible maximum value of SDI, and s = number of species in a sample. D for a sample containing s species is minimum when each species has a same number of individuals or $p_i = 1/s$. In that case,

$$D = \Sigma(p_i)^2 = (p_1)^2 + (p_2)^2 + \ldots + (p_s)^2 = s(1/s)^2 = 1/s.$$

Besides ESDI, species dominance (SD) was also used as evenness index. In this analysis, SD was expressed as the relative abundance of the three most abundant species:

$$\text{SD} = p_1 + p_2 + p_3,$$

where p_1 = proportion of the most abundant species in a sample, p_2 = proportion of the second most abundant species, and p_3 = proportion of the third most abundant species. As in the other analyses, SDI, ESDI, and SD were calculated using fish monitoring data from each site with five or more gill nets.

In conducting all regression analyses on log (MNFPN), Simpson's Diversity Index (SDI), evenness (ESDI), and species dominance (SD), three regression assumptions were also tested: heteroscedasticity (with a White test), first-order positive autocorrelation (with a Durbin-Watson statistic), normality of error terms (with a Shapiro-Wilks statistic; SAS, 2008). In all analyses, $p < 0.05$ was required for significance.

RESULTS

Overall Trends in Fish Catches

Substantial yearly fluctuations in total fish catches (MNFPN) for aggregate species were observed within each stratum. However, NS1 consistently had the highest catches, followed by NS2 and CGR. Total aggregate fish catches (MNFPN) in NS1 ranged between 16.9 in 1959 and 136.9 in 1994, in NS2 between 12.0 in 1961 and 44.4 in 1993, and in CGR between 10.9 in 1976 and 66.3 in 1980. Consistent with the complete standardization in gillnets starting in 2000, total aggregate fish catches in each of the three strata showed fewer fluctuations than corresponding catches for the years before 2000 (NS1: range 29.2 in 2008 to 59.3 in 2000, NS2: 15.6 in 2008 to 41.9 in 2002, CGR: 11.0 in 2008 and 2011 to 22.7 in 2003.

Natural log of aggregate catches (log (MNFPN)) showed significant declines in CGR, NS1, and NS2 (Table 2; Figure 2). Scatter plots also showed a change of trends, from increasing to decreasing numbers of fish, in NS1, NS2, and CGR prior to and

Table 2 Summary of linear regression equations results, degrees of freedom (df) for trends (+/−) in catches and testing three regression assumptions (heteroscedasticity, positive first-order autocorrelation, normality of error) in Noxon Stratum 1 (NS1), Noxon Stratum 2 (NS2) and Cabinet Gorge Reservoir (CGR), various years, 1955–2011

								Test of Linear Regression Assumptions			
								Heteroscedasticity	Autocorrelation		Normality
Figure	Dependent variable	Period	Site	df	Trend	r^2	p-value	(Pr > Chi Sq)[1]	(DW	Pr < DW)[2]	(Pr < W)[3]
Fig. 2	Log(MNFPN)	1959–1993	NS1	20	+	0.27	0.016*	0.788	2.32	0.696	0.838
			NS2	12	+	0.10	0.305	0.833	2.62	0.806	0.893
			CGR	22	−	0.02	0.558	0.434	2.00	0.403	0.968
		1994–2011	NS1	12	−	0.60	0.002*	0.387	1.79	0.228	0.898
			NS2	9	−	0.53	0.017*	0.186	2.50	0.668	0.399
			CGR	10	−	0.55	0.009*	0.098	2.73	0.828	0.886
Fig. 3	Log(MNFPN) for Yellow perch	1955–1993	NS1	20	+	0.40	0.002*	0.682	1.77	0.216	0.330
			NS2	12	+	0.38	0.025*	0.298	2.57	0.776	0.633
			CGR	22	+	0.19	0.036*	0.504	2.04	0.450	0.012*
		1994–2011	NS1	12	−	0.55	0.004*	0.470	1.59	0.131	0.823
			NS2	9	−	0.40	0.050	0.177	2.28	0.525	0.549
			CGR	10	−	0.39	0.041*	0.632	2.40	0.628	0.501
N/A	Log(MNFPN) for Longnose sucker	1955–2011	NS1	27	−	0.58	<0.001*	0.047*	1.90	0.321	0.024*
			NS2	15	−	0.69	<0.001*	0.327	2.37	0.687	0.998
			CGR	27	−	0.49	<0.001*	0.142	1.88	0.297	0.761
Fig. 4	Log(MNFPN) for Largescale sucker	1955–2011	NS1	33	−	0.32	<0.001*	0.490	1.52	0.053	0.001*
			NS2	22	−	0.20	0.031*	0.124	1.47	0.061	0.166
			CGR	33	−	0.47	<0.001*	0.236	1.94	0.360	0.038*
Fig. 5	Log(MNFPN) for Peamouth	1955–1993	NS1	18	+	0.48	0.001*	0.122	2.36	0.711	0.893
			NS2	11	+	0.43	0.020*	0.041*	1.32	0.050	0.743
			CGR	22	+	0.04	0.389	0.615	1.74	0.187	0.365
		1994–2011	NS1	12	−	0.74	<0.001*	0.726	2.16	0.485	0.297
			NS2	9	−	0.51	0.020*	0.573	2.91	0.884	0.139
			CGR	10	−	0.53	0.011*	0.396	2.08	0.403	0.489
Fig. 6	Log(MNFPN) for Northern pike	1971–2011	NS1	12	+	0.87	<0.001*	0.933	2.92	0.934	0.140
			NS2	12	+	0.55	0.004*	0.059	2.15	0.490	0.989
			CGR	9	+	0.13	0.315	0.287	1.39	0.073	0.855
Fig. 7	Log(MNFPN) for Walleye	2000–2011	NS1	9	+	0.50	0.022*	0.206	2.82	0.849	0.753
			NS2	7	+	0.03	0.680	0.306	1.44	0.077	0.314
			CGR	5	+	0.17	0.417	0.489	1.05	0.003*	0.376
N/A	Log(MNFPN) for Smallmouth bass	1987–2011	NS1	17	+	0.49	0.001*	0.042*	2.36	0.695	0.501
			NS2	9	·	0.01	0.807	0.331	3.02	0.929	0.438
			CGR	9	·	0.01	0.826	0.407	2.69	0.786	0.009*
N/A	Log(MNFPN) for Largemouth bass	1955–2011	NS1	24	+	0.15	0.059	0.864	1.78	0.218	0.400
			NS2	5	−	0.09	0.564	0.136	2.14	0.367	0.634
			CGR	14	−	0.16	0.146	0.138	1.09	0.011*	0.956
N/A	Log(MNFPN) for Northern pikeminnow	1955–1993	NS1	19	+	0.12	0.133	0.125	1.06	0.005*	0.135
			NS2	11	+	0.04	0.543	0.236	2.36	0.618	0.906
			CGR	22	−	0.01	0.655	0.136	1.16	0.008*	0.181
		1994–2011	NS1	12	−	0.63	0.001*	0.252	2.17	0.493	0.537
			NS2	9	−	0.35	0.070	0.301	1.60	0.135	0.700
			CGR	10	·	0.01	0.726	0.623	2.51	0.704	0.452
Fig. 8	Log(MNFPN) for Bull trout	1955–1999	NS1	21	−	0.60	<0.001*	0.166	2.05	0.454	0.752
			NS2	9	−	0.43	0.040*	0.060	1.36	0.064	0.816
			CGR	19	−	0.58	<0.001*	0.408	2.16	0.548	0.555
N/A	Log(MNFPN) for Rainbow trout	1955–1999	NS1	19	−	0.53	<0.001*	0.085	2.10	0.492	0.311
			NS2	9	−	0.57	0.011*	0.199	1.81	0.236	0.374
			CGR	16	−	0.16	0.114	0.188	1.58	0.115	0.218
N/A	Log(MNFPN) for Brown trout	1958–1999	NS1	20	+	0.13	0.109	0.456	1.14	0.009*	0.005*
			NS2	11	−	0.70	<0.001*	0.539	2.56	0.751	0.650
			CGR	22	+	0.14	0.078	0.392	1.19	0.011*	0.717
N/A	Log(MNFPN) for Lake whitefish	1955–1993	NS1	20	−	0.27	0.016*	0.965	1.70	0.172	0.793
			NS2	12	+	0.05	0.483	0.396	1.29	0.042*	0.260
			CGR	21	+	0.19	0.041*	0.315	1.71	0.175	0.889
		1994–2011	NS1	12	−	0.30	0.053	0.419	1.78	0.226	0.505

(Continued on next page)

Table 2 Summary of linear regression equations results, degrees of freedom (df) for trends (+/−) in catches and testing three regression assumptions (heteroscedasticity, positive first-order autocorrelation, normality of error) in Noxon Stratum 1 (NS1), Noxon Stratum 2 (NS2) and Cabinet Gorge Reservoir (CGR), various years, 1955–2011 *(Continued)*

								Test of Linear Regression Assumptions			
								Heteroscedasticity	Autocorrelation		Normality
Figure	Dependent variable	Period	Site	df	Trend	r^2	p-value	(Pr > Chi Sq)[1]	(DW	Pr < DW)[2]	(Pr < W)[3]
			NS2	9	−	0.08	0.427	0.393	2.15	0.436	0.603
			CGR	8	−	0.29	0.137	0.211	1.73	0.188	0.709
N/A	Log(MNFPN) for Mountain whitefish	1955–2011	NS1	20	−	0.29	0.012*	0.349	2.18	0.569	0.134
			NS2	11	−	0.18	0.169	0.453	2.14	0.460	0.578
			CGR	23	−	0.36	0.002*	0.078	2.29	0.690	0.876
N/A	Log(MNFPN) for Pumpkinseed	1955–2011	NS1	3	+	0.43	<0.001*	0.099	2.20	0.653	0.042*
			NS2	14	+	0.14	0.169	0.246	3.19	0.991	0.031*
			CGR	25	+	0.01	0.567	0.045*	2.22	0.642	0.942
N/A	Log(MNFPN) for Bullhead	2000–2011	NS1	9	−	0.23	0.156	0.203	1.23	0.036*	0.141
			NS2	9	−	0.48	0.026*	0.165	2.85	0.860	0.770
			CGR	N/A							
Fig. 9	Log(MNFPN) for FORAGE group	1955–1993	NS1	20	+	0.31	0.009*	0.592	1.47	0.063	0.005*
			NS2	12	+	0.28	0.061	0.410	2.28	0.580	0.956
		CGR	22	·		0.00	0.902	0.279	2.10	0.506	0.549
		1994–2011	NS1	12	−	0.64	0.001*	0.489	1.71	0.185	0.927
			NS2	9	−	0.51	0.020*	0.194	2.40	0.605	0.102
			CGR	10	−	0.62	0.004*	0.209	2.36	0.599	0.528
Fig. 10	Log(MNFPN) for PREDATOR group	1955–1993	NS1	13	+	0.12	0.218	0.746	0.77	0.001*	0.354
			NS2	3	+	0.26	0.486	0.135	2.91	0.741	0.897
			CGR	9	+	0.01	0.794	0.127	1.70	0.177	0.524
		1994–2011	NS1	12	+	0.53	0.005*	0.235	2.70	0.846	0.355
			NS2	9	+	0.00	0.864	0.057	1.81	0.231	0.276
			CGR	9	+	0.52	0.018*	0.414	1.07	0.016*	0.916
N/A	Log(MNFPN) for TROUT group	1955–1993	NS1	20	−	0.36	0.004*	0.337	1.33	0.030*	0.217
			NS2	11	−	0.86	<0.001*	0.493	2.16	0.476	0.305
			CGR	22	−	0.19	0.037*	0.462	1.90	0.318	0.253
		1994–2011	NS1	9	−	0.30	0.104	0.059	1.43	0.077	0.725
			NS2	N/A							
			CGR	10	−	0.60	0.005*	0.756	2.01	0.359	0.748
N/A	Simpson's Diversity Index	1955–1993	NS1	20	−	0.16	0.073	0.724	1.11	0.007*	0.245
			NS2	12	−	0.60	0.002*	0.142	2.25	0.559	0.116
			CGR	22	−	0.04	0.383	0.298	1.92	0.331	0.020*
		1994–2011	NS1	12	+	0.60	0.002*	0.559	0.68	0.000*	0.366
			NS2	9	+	0.34	0.075	0.274	1.92	0.293	0.398
			CGR	10	+	0.07	0.420	0.268	1.84	0.251	0.611
N/A	Evenness Index- Simpson's Diversity Index	1955–1993	NS1	20	−	0.20	0.045*	0.885	1.15	0.009*	0.442
			NS2	12	−	0.44	0.014*	0.286	2.48	0.718	0.212
			CGR	22	−	0.03	0.461	0.133	2.20	0.596	0.039*
		1994–2011	NS1	12	+	0.58	0.003*	0.521	0.70	0.001*	0.349
			NS2	9	+	0.28	0.114	0.301	2.07	0.386	0.068
			CGR	10	+	0.03	0.583	0.245	1.89	0.281	0.373
N/A	Dominance	1955–1993	NS1	20	+	0.33	0.007*	0.456	1.49	0.072	0.671
			NS2	12	+	0.69	<0.001*	0.199	2.36	0.634	0.841
			CGR	22	+	0.11	0.122	0.045*	1.39	0.038*	0.865
		1994–2011	NS1	12	−	0.69	<0.001*	0.716	1.55	0.114	0.270
			NS2	9	−	0.41	0.045*	0.367	2.15	0.435	0.948
			CGR	10	·	0.00	0.980	0.267	1.74	0.197	0.415

An asterisk (*) indicates statistical significance at $p < 0.05$.

(Pr > ChiSq)[1] denotes a p-value for testing the null hypothesis that the variance of the residuals is homogenous.

(DW Pr < DW)[2] denotes Durbin-Watson statistic (**DW**) and p-value for positive first-order correlation (**Pr < DW**).

(Pr < W)[3] denotes a p-value from the Shapiro-Wilks statistic for testing normality of error terms.

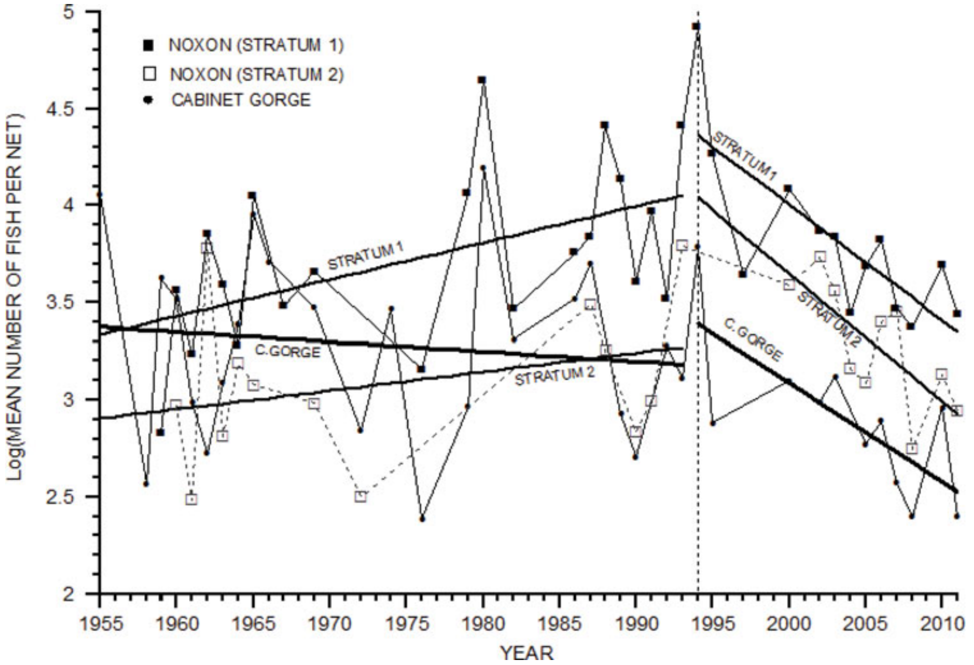

Figure 2 Log(mean number of fish per net; all species combined) for Noxon Stratum 1 (NS1), Noxon Stratum 2 (NS2), and Cabinet Gorge Reservoirs, 1955–2011.

after the year 1994. Overall, log catches before 1994 showed no significant trends in NS2 or CGR ($p > 0.05$), but increased significantly over that period in NS1 ($r^2 = 0.27$; $p = 0.016$; Figure 2). However, total log catches in NS1, NS2, and CGR all decreased significantly from 1994 to 2011 ($p < 0.05$; Figure 2; Table 2).

Trends in Species Catches

In CGR, the same four species were the most commonly caught over the periods 1955–1959, 1972–1993, and 1994–2011: peamouth, northern pikeminnow, yellow perch, and largescale sucker. These same species also ranked at or near the top in the NS1 and NS2.

Trends for species and species groups showed some clear patterns (Table 2). For forage species, yellow perch log catches increased significantly until 1994 in NS1, NS2, and CGR ($p = 0.002$, 0.025, and 0.036, respectively) but decreased significantly over the period 1994–2011 ($p = 0.004$, 0.050, and 0.041, respectively). Longnose suckers and largescale suckers showed significant declines ($p < 0.0001$ for longnose suckers, Table 2; $p = 0.0005$, 0.0305, and < 0.0001 for largescale suckers (Table 2) in log catches over the entire reservoir periods in all three strata. In addition, peamouth increased significantly in NS1 and NS2 ($p = 0.0011$ and 0.0203, respectively; Table 2) through 1993 but decreased significantly in all NS1, NS2, and CGR ($p = 0.0002$, 0.0195, and 0.0111, respectively; Table 2) over the period 1994–2011.

Trends of predators, especially non-native predators, contrasted with trends in the forage species. Over the period 1971–2011, northern pike log catches increased significantly in NS1 and NS2 ($p < 0.0001$ and $p = 0.0037$, respectively; Table 2). Walleye increased significantly ($p = 0.0221$; Table 2) in NS1 since 2000 as did smallmouth bass in NS1 in NS1 since 1987 ($p = 0.0013$; Table 2). No trends were detected in largemouth bass (Table 2). Northern pikeminnow decreased significantly since 1994 in NS1; no other significant trends in this species were detected in NS2 or CGR (Table 2).

Trends in salmonids were difficult to characterize as a group because of changes in sampling protocols to avoid them starting in 2000 and the scarcity of most species in catches. The catch results must, therefore, be interpreted with caution. However, a significantly decreasing trend was noted for bull trout up to 2000 in NS1 ($p < 0.0001$), NS2 ($p = 0.0401$), and CGR ($p < 0.0001$; Table 2). Rainbow trout also declined significantly in NS1 ($p = 0.0003$) and NS2 ($p = 0.0113$), but not in CGR ($p = 0.1139$; Table 2). Brown trout decreased significantly over the period through 1999 in NS2 ($p = 0.0007$), but showed no significant trends in NS1 ($p = 0.1085$) or CGR ($p = 0.0779$; Table 2). Lake whitefish showed significant increases in CGR and NS1 before 1994 ($p = 0.0160$ and 0.0405, respectively; Table 2); after 1994 log catches trended downward but did not reach statistical significance (Table 2). Mountain whitefish declined significantly ($p = 0.0124$) in NS1 and in CGR ($p = 0.0020$) over the entire reservoir period (Table 2). Pumpkinseed increased significantly over the entire period in NS1 ($p < 0.0001$; Table 2); bullhead decreased significantly in NS2 since 2000 ($p = 0.0257$; Table 2). Cutthroat trout, brook trout, and kokanee were caught too rarely for discernible trends.

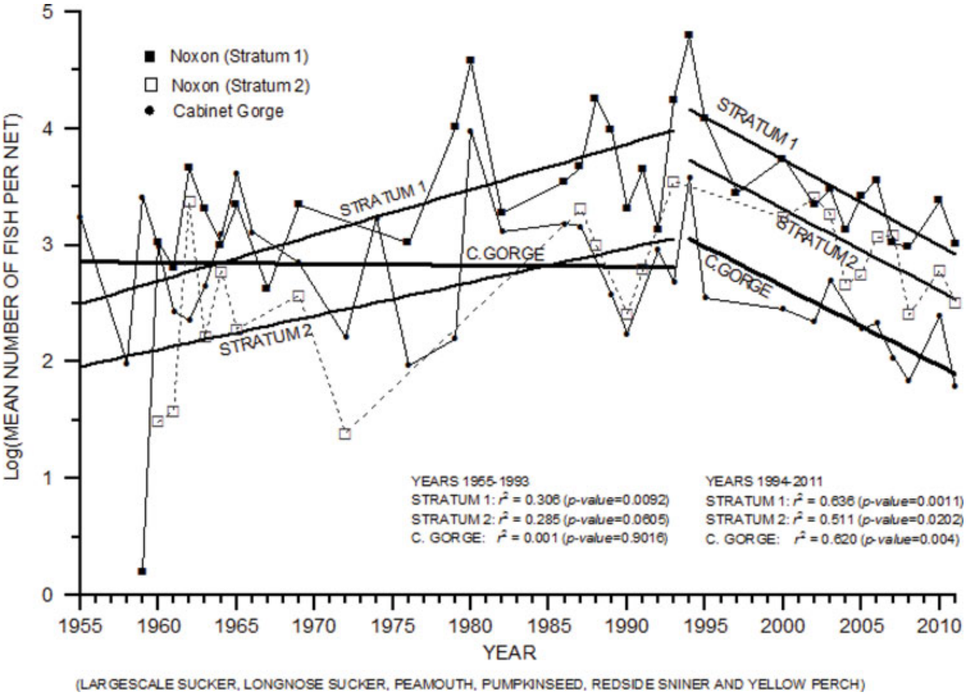

Figure 3 Log (mean number of fish per net) for Forage Group for Noxon Stratum 1 (NS1), Noxon Stratum 2 (NS2), and Cabinet Gorge Reservoirs, 1955–2011.

Trends in Species Groups

Significant declines in the Forage Group were found in NS1, NS2, and CGR ($p = 0.0011$, 0.0202, and 0.0040, respectively, over the period 1994–2011 (Table 2, Figure 3). These declines followed a significant increase in this group prior to 1993 in NS1 ($p = 0.0092$) and a non-significant increasing trend in NS2 ($p = 0.06$; Table 2; Figure 3). In contrast, the Non-native Predator Group showed significant increases in NS1 and CGR ($p = 0.0049$ and 0.0178, respectively; Table 2) over the period 1994–2011, but no significant trends during the earlier period (Figure 4). The Trout Group, although difficult to interpret as indicated, declined significantly or highly significantly in all three strata during the period through 1993 (Table 2).

Additional insight was gained from viewing the trends in the ratios of fish in these three groups to the total catches. The Non-native Predator Group increased strongly as a percentage of total aggregate fish catch since 1994, constituting the most obvious change in the fish community (Figure 5). The Forage Group and the Trout Group trended downward (Table 2). For CGR, the log (MNFPN) for the Forage Group was also significantly inversely related to the log (MNFPN) for the Non-native Predator Group ($r = -0.51$; $p = 0.02$; $N = 20$; Figure 6).

Diversity and Evenness

Simpson's's diversity index depicted no significant decrease in diversity ($p = 0.07$) in NS1 and NS2 from reservoir filling until 1993 and a significant increase in diversity from 1994 through 2011 (Table 2). Evenness in these strata decreased over the period through 1993, and dominance increased, as the reservoir became more dominated by some abundant forage species such as yellow perch and peamouth. Over the period 1994–2011, this pattern was reversed as the forage species declined and dominance decreased (Table 2). In only three of 19 years was there not at least one significant difference in diversity among the three strata (1961, 2005, and 2006).

Regression Assumptions

Of 102 regression equations developed, only 5 showed significant heteroscedasticity, 16 showed significant positive first-order autocorrelation, and 11 failed normality of error (Table 2). Overall, these violations were considered acceptable in applying linear regression models to the data.

DISCUSSION

In CGR and Noxon (NS1 and NS2), results of gillnet catches depict a decline in several forage species in absolute and relative abundance associated with a concurrent increase in non-native piscivorous predators. This shift has become especially apparent since the mid-1990s. Catches of forage species as a group, yellow perch, longnose suckers, largescale suckers, and peamouth have declined. Catches of salmonids also appear to have declined over the long and shorter terms, including bull trout (before 2000) and brown trout.

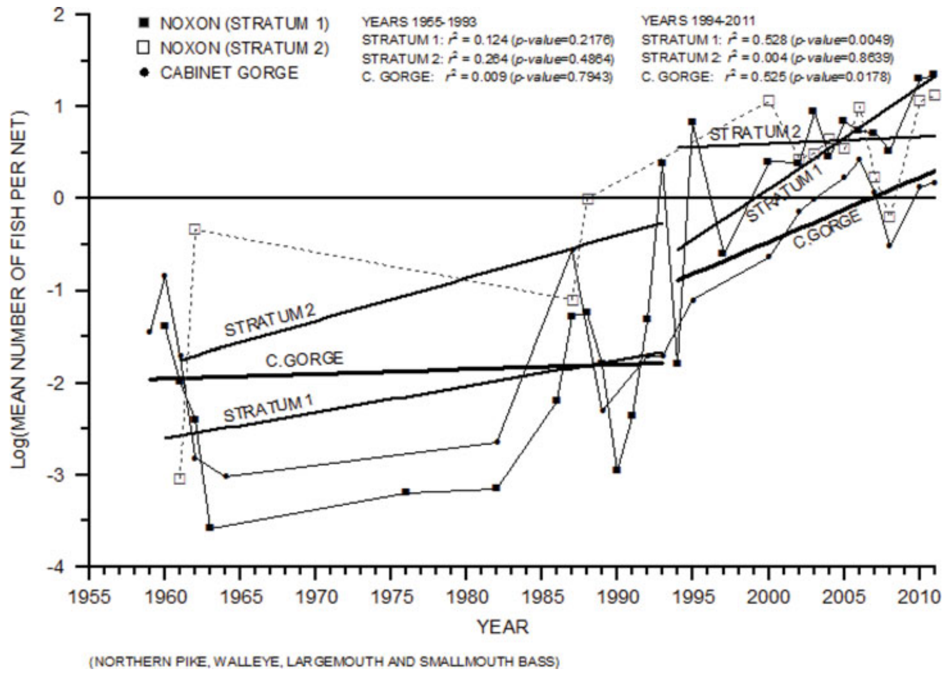

Figure 4 Log (mean number of fish per net) for Non-native Predator Group for Noxon Stratum 1 (NS1), Noxon Stratum 2 (NS2), and Cabinet Gorge Reservoirs, 1955–2011.

In contrast, the aggregate catches of the non-native predators have increased greatly as a group (Figure 4) and most dramatically as a percentage of the total catch since the 1990s (Figure 5), including increases in catches of walleye and northern pike. Noxon had higher numbers of walleye than Cabinet Gorge, consistent with the more reservoir-like environment of Noxon favored by this species. Telemetry studies of Horn et al. (2009) found that most of the telemetered walleye in Noxon inhabited the more reservoir–like portion (NS1) for most of the year. Additionally, the high use of areas near the mouths of bull trout rearing tributaries found in that study represents a potential predation risk to migratory salmonids. Walleye have been shown to consume salmonids in several studies within the region (e.g., Vigg et al., 1991; Baldwin et al., 2003). The large

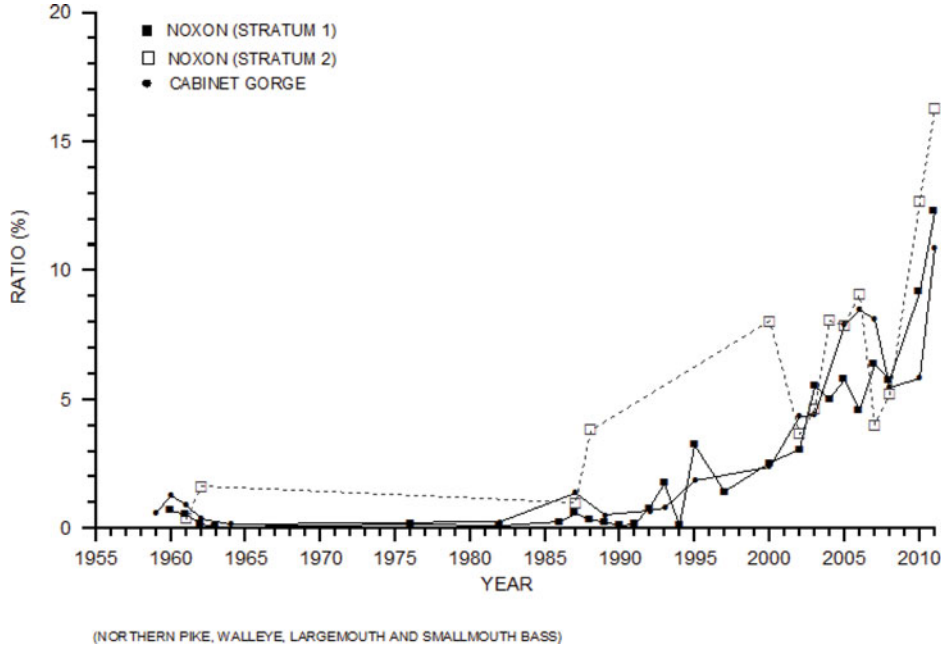

Figure 5 Ratio of fish in the Non-native Predator Group to total fish catch for Noxon Stratum 1 (NS1), Noxon Stratum 2 (NS2), and Cabinet Gorge Reservoirs, 1955–2011.

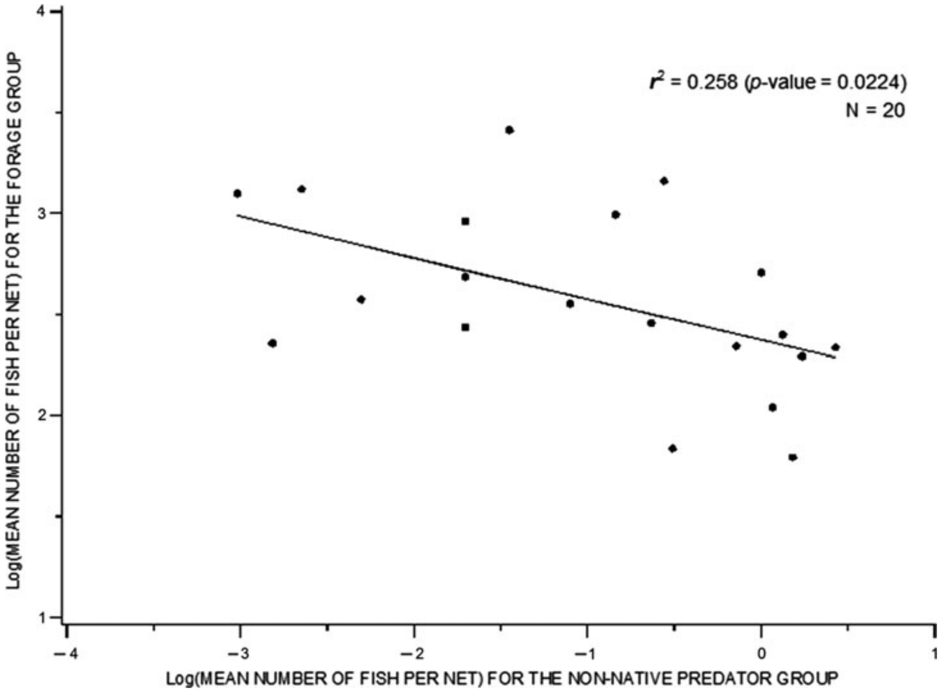

Figure 6 Relationship between log (mean number of fish per net) for the Forage Group and log (mean number of fish per net) for the Non-native Predator Group, Cabinet Gorge Reservoir.

maximum size of northern pike present a potential predation risk for multiple age classes of migratory bull trout, and condition of pike was found to be high (relative weights well over 100), especially in Cabinet Gorge (Liermann and Tholl, 2003; Hanson and Tholl, 2007; Storaasli and Moran, 2012a). In addition, pike were found to inhabit areas of Cabinet Gorge frequented by bull trout (Bernall and Moran, 2005). The trends for bass, although not clearly indicated except for significant increases in smallmouth bass in NS1, must be interpreted cautiously because bass are not highly susceptible to being caught with gillnets. Horn and Tholl (2010) analyzed bass reproduction and fish tournament data which suggested possible increases in largemouth bass, although other data, preferably from electrofishing, should be used to assess trends in abundance.

In contrast to non-native predator increases, abundance of the native predator northern pikeminnow has not trended upward (Table 2). This species can function both as predator and, at smaller sizes, as prey (Vigg et al., 1991). Past studies indicate that pikeminnows are slow growing, eat primarily crayfish, and thus act as forage fish up to about age-4 (Washington Water Power, 1996b).

As a result of the additional non-native species and their increases, species diversity has, overall, trended upward, whereas species dominance based on the three most abundant species has decreased, as previously abundant forage species have been reduced and greater evenness has resulted. Overall, the fish community in the reservoirs has shifted from a natural, more riverine system (pre-impoundment) to an unnatural, coldwater-managed (i.e., salmonid stocked) system in the 1950s through the 1970s, to a system dominated by forage species (and one native piscivore, northern pikeminnow) in the 1980s and early 1990s, and, most recently, to a system more strongly structured by non-native piscivores in the twenty-first century.

The statistically significant increases in northern pike and walleye observed in this study, as well as the decreases in forage, are familiar occurrences in regional reservoirs. McMahon and Bennett (1996), in a thorough review to that time of the potential effects of walleye and northern pike on native fauna of the northwest, noted the tendency of such introductions, whether planned or not, to result in predator traps, i.e., an increase in the predators and a decline in forage, often to the point that alternative fish such as stocked salmonids can be affected (Vigg et al., 1991; Baldwin et al., 2003). These authors also noted the tendency for such piscivores to be favored by the water management strategies implemented in many reservoirs; drawdowns can reduce aquatic macrophytes (and forage cover), concentrate prey, and increase vulnerability. However, in Noxon, since the reduction in large drawdowns, macrophytes have increased (S. P. Moran, Avista Utilities, personal communication), providing some refuge for prey and also successful northern pike spawning.

The particular non-native predator and native prey species that may interact to the detriment of the native species will depend on a range of factors, including habitat conditions and fish morphology (e.g., spiny or soft-rayed; Whittier and Kincaid, 1999). Although no detailed food web studies are available for CGR or Noxon to identify causal mechanisms, the declines in total numbers of forage fish, as well as of several important forage species such as yellow perch, peamouth, and native suckers are consistent with the idea of a shift toward a higher number of non-native piscivores eating the forage fish, reducing their numbers, and the predators thus becoming a more dominant component of the fish community. The new reservoir habitat may have created open niches for non-native species, as suggested by the higher abundance of forage fishes in the 1980s and 1990s before predator introductions and higher predator populations afterward. Although such speculations are plausible, as McMahon and Bennett (1996) noted, more detailed monitoring studies are needed on predator–prey interactions after introductions of non-native species. Such studies may need to delve into the food webs beyond the level of other fish species to look at both direct and indirect effects of the introduction of the non-native predator (e.g., Nyström et al., 2001).

The observed statistically significant declining trends in salmonid catches are clear before 2000, but must be interpreted with caution since 2000. The recent emphasis away from salmonid sampling was particularly pronounced in the case of bull trout. Removal of gillnet sites, where trout had been captured in earlier sampling, was enacted after 1999 due to concerns about lethality following species listing. Although bull trout declined significantly from reservoir construction through 1999, bull trout redd surveys conducted along the major tributaries of CGR and Noxon conducted since 2001 have shown variable numbers with a recent increasing trend in Noxon tributaries (Storaasli and Moran, 2012b). It is known that the Lower Clark Fork River mainstem was not optimal salmonid habitat even before impoundment, and that declines in quantity and quality of salmonid habitat associated with impoundment prevented the development of successful salmonid fisheries, despite considerable long-term effort (Huston, 1985; Horn and Tholl, 2010).

The community structure changes observed in the Noxon and CGR differ from trends observed in other lentic waters because of distinct differences in physical changes before and after impoundment, differential effects on individual species, and the particular species present (e.g., La Porta et al., 2010; Mehner, 2010). Specific characteristics of the water bodies (reservoirs versus natural lakes) and of native versus non-native (i.e., novel) predators and prey in different situations will dictate or influence outcomes of specific predator prey-interactions. In Noxon and CGR, existing mainstem and reservoir conditions and habitat changes have not favored recovery of bull trout but have favored the expansion of coolwater and some warmwater species, especially non-native piscivores. This reality will continue to affect success of restoration efforts for bull trout, even as progress is made in tributaries and in fish trap and haul efforts and proposed fish passage at the dams.

In all of our analyses, conclusions were made with consideration of the community composition data being influenced by differential susceptibility of various fish species to capture with gillnets. For example, Huston (1985) noted that intensive sampling of shoreline and pelagic areas in May–Oct 1976 showed that pikeminnows and peamouths made high use of nearshore areas. Such distribution may over-represent them in samples. Similarly, the low susceptibility of bass to gillnets makes interpretation of the sampling results inadvisable for all but basic questions of presence or absence. Bass were not abundant in gillnet catches, even though populations are large enough to result in several professional and semi-professional tournaments each year (Liermann and Tholl, 2003). Although bass recruitment monitoring and bass tournament monitoring are conducted (Liermann and Tholl, 2003) more reliable information on bass status is needed. Most other species are probably sampled more reliably with gillnets. Merwin trapping has also been highly successful for northern pikeminnow, peamouth, and yellow perch (Liermann and Tholl, 2003; Bernall and Moran, 2005), although the efficiency of this gear was not evaluated for most species and sampling is not conducted yearly. Based on comparisons of fyke and Merwin northern pike catches to gill net captures of this species in CGR, Storaasli and Moran (2012a) suggested that gill net trends were sufficient to depict overall trends for this species as had been observed by Pierce et al. (2010) for Minnesota lakes. The effects of gear biases (Hubert, 1996) are best addressed by using a variety of gears to more adequately assess overall fish community composition. Overall, however, observed trends within species would be expected to have less bias, and our conclusions for the community change (e.g., more non-native piscivores) would therefore be generally applicable to individual species as well (e.g., northern pike, walleye).

Management Implications

A major issue confronting management agencies is the need for well-articulated philosophies and appropriate policies guiding management of non-native predator species and entire novel (native and non-native) fish communities as a whole (Simberloff et al. 2005). Among non-native fish species, the most problematic in terms of policy development are those already introduced into a basin shown to cause damage or harm in some situations and locations, but that have perceived benefits (e.g., as game fish) that militate against eradication or reduction actions (e.g., Copp et al. 2005). For example, some introductions of non-native game fish have resulted in decimation of native fauna and diversity (lake trout *Salvelinus namaycush* in several locations in the western U. S., Martinez et al. 2009; Nile perch *Lates niloticus* in Africa, Stiassny, 1996; peacock bass *Cichla kelberi* in Rosana Reservoir, Brazil, Pelicice and Agostinho, 2009). Recent adoptions of lake trout suppression in Yellowstone National Park, Lake Pend Oreille, Swan Lake, and other locations (Martinez et al., 2009) have been based on their negative impacts on native fish. Yet in other situations, non-natives are tolerated and even enhanced (Independent Scientific Advisory Board, 2008). In some instances, the effects of non-natives are often not known, which may result in no action being taken toward them. The current inconsistent strategy for non-native species in management situations within the Columbia basin, most obviously for such problematic species as walleye, northern pike, and the basses, reflects ambiguous attitudes by the public and the co-managers toward those species. Managing problematic species entails not only managing their distribution, abundance, and productivity, but also considering their human societal context, including divergent public opinion (García-Llorente et al., 2008) and resulting illegal (non-agency) stocking actions. Beyond ecological considerations, the relative social values attributed to native and non-native predators are typically within the realm of social or political science (Rosenzweig, 2001).

Much remains to be learned about the structure and function of the novel communities. Gido and Brown (1999) concluded from their broad analysis of North American fauna that "the result [of species introductions] has been a net increase in fish species richness in most drainages because the number of colonizations by alien species has exceeded the number of extinctions of native species .... [M]ost communities in nature are not saturated with species..." (p. 394). Knowing how the non-native species interact in altering the functioning of the ecosystem is critical to understanding the long-term effects on native fauna. Results from our study show that although native diversity has decreased, total diversity has not. In managing these newly formulated systems containing native and non-native species more information is needed on their food webs (McMahon and Bennett, 1996; Naiman et al., 2012) and on factors such as water level changes as they affect year class strengths of individual species and species groups.

How to manage the novel communities and their newly constituted diversity presents a formidable challenge for managers, especially with ESA-listed species and diverse public interests (Hobbs et al., 2006; Hobbs, 2007; Lindenmayer et al., 2008). In our view, problems with non-natives have been pervasive enough that in instances where non-native removal or effective suppression is possible, that course should be pursued. However, the views of the appropriate future role of non-native species, especially ones already established in an area, are often strongly polarized for some problematic species and will probably remain so. In our rapidly changing human society and landscapes, the long-term relationships and roles of native and non-native fishes in habitats such as Noxon and CGR remain unclear. Schlaepfer et al. (2011) suggest that "non-native species could come to fill important ecosystem and aesthetic functions, particularly in places where native species cannot persist due to environmental changes ... it seems likely that non-native species will often contribute to some of the putative benefits of species rich ecosystems, such as increased productivity and stability... but this proposition has not been tested" (p. 433). More information is needed on the benefits, costs, and feasibilities of removing, suppressing, acquiescing to, or in rare instances enhancing non-natives in various situations (Gozlan et al., 2010). In some situations, ecologists may be advised to assess how non-natives may provide ecosystem services and functions formerly provided by native species (Lindenmayer, 2008; Carroll, 2011). We need science-based methodologies for assessing risk before and after non-native introductions (McMahon and Bennett, 1996; Wilcove et al., 1998; Gozlan et al., 2010). Future efforts will need to more effectively consider the linkages between reservoirs, their rapidly changing habitat and fauna, and other relevant landscape features (Moyle and Light, 1996; Miranda, 2008). More consideration will be needed on the roles newly established species may play in effective fisheries management plans serving the public interest (Seastedt et al., 2008).

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