Population Structure and Dynamics of Northern Pike and Smallmouth Bass in Coeur d'Alene Lake, Idaho

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Source: Northwest Science, 89(3):280-296.
Published By: Northwest Scientific Association
DOI: http://dx.doi.org/10.3955/046.089.0308
URL: http://www.bioone.org/doi/full/10.3955/046.089.0308

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Abstract

Numerous species have been introduced to Coeur d'Alene Lake, Idaho over the last century, but minimal research has been completed to understand their population dynamics. The objective of this study was to describe the population demographics and dynamics of northern pike (*Esox lucius*) and smallmouth bass (*Micropterus dolomieu*), two important nonnative sport fishes in the system to provide information that will assist with guiding management decisions. The oldest northern pike was age 7 and the oldest smallmouth bass was age 11. Populations of both species exhibited very stable recruitment with a recruitment coefficient of determination of 0.99 for northern pike and 0.98 for smallmouth bass. Total annual mortality was estimated as 66% for northern pike and 42% for smallmouth bass. Growth of northern pike in Coeur d'Alene Lake was comparable to the 50–75th percentiles of growth exhibited by lentic northern pike populations across North America. Northern pike in Coeur d'Alene Lake were most similar to populations in the north-central and northeast United States with fast growth rates and short life spans. In contrast, smallmouth bass grew slowly and generally fell within the 5th percentile of lentic smallmouth bass populations in North America. Smallmouth bass in Coeur d'Alene Lake were similar to other populations in northern regions of the United States displaying slow growth rates with high longevity. Results of this study provide important insight on nonnative northern pike and smallmouth bass population dynamics.

Keywords: northern pike, smallmouth bass, demographics, dynamics, size, growth

Introduction

The introduction of fishes into systems outside their native distribution has occurred for centuries throughout the world (Gozlan et al. 2010). North America is no exception where nonnative species outnumber native species in some systems (Horak 1995). A multitude of reasons are responsible for species introductions; however, most fishes have been introduced to meet societal desires (Cambray 2003). Nonnative fishes have also been dispersed unintentionally via live bait releases, escapes from aquaculture operations, and the release of pets. Historically, government agencies or other entities deliberately introduced species to provide a food resource (Fuller et al. 1999). More recently, deliberate stockings have occurred to create or supplement a fishery, as a biomanipulation tool, and for conservation efforts. Although not all introductions result in self-sustaining populations, some species become abundant and cause substantial negative ecologic and economic effects (Kolar et al. 2010). Nonnative species pose challenges for natural resource management and an understanding of the population dynamics of nonnative species is critical for guiding management actions.

Information on population dynamics or rate functions (i.e., mortality, growth, and recruitment) is used in nearly every aspect of fisheries management. Growth integrates internal (e.g., genetics) and external (e.g., habitat and prey availability) factors, and has been used to evaluate habitat suitability, prey availability, and the influence of management activities (Quist et al. 2012). Esti-

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mates of mortality are essential for assessing fish populations, particularly in exploited populations (Allen and Hightower 2010). Another important rate function that is one of the most variable and difficult functions to quantify is recruitment (Isermann et al. 2002, Quist 2007). While each of these functions is important, information on all aspects of fish population dynamics is central to making informed management decisions. Nonnative species are of particular interest because factors influencing their population dynamics are likely quite different than in areas where they are native.

Two common nonnative species in western North America are northern pike (*Esox lucius*) and smallmouth bass (*Micropterus dolomieu*). Northern pike are top-level piscivores with a circumpolar distribution. They are a mesothermal fish that occurs across a wide range of environmental conditions; however, they prefer shallow and vegetated habitats (Casselman and Lewis 1996, Craig 2008). Their popularity as a sport fish prompted northern pike to be introduced to systems across North America (Crossman 1978). In addition to being stocked for sport-fishery enhancement, they have also been introduced as a biomanipulation tool (Pflieger 1997). Smallmouth bass have a native distribution spanning from the Great Lakes and St. Lawrence River south to the Mississippi River and its tributaries (Page and Burr 1991, Carey et al. 2011). Like northern pike, smallmouth bass are a popular sport fish and have been stocked throughout North America (Carey et al. 2011). In addition to frequent and widespread introductions, the success of smallmouth bass outside their native distribution is attributed to their ability to thrive in diverse habitats (Coble 1975, Brown and Bozek 2010).

Northern pike and smallmouth bass were introduced both legally and illegally in Idaho as a result of growing interest by anglers for coolwater and warmwater sport fisheries (Dillon 1992). Little is known about the illegal introduction of northern pike to Idaho, but they were first encountered in floodplain lakes along the Coeur d'Alene River, known as the "chain lakes" in the early 1970s (Rich 1992). The availability of prey items and quantity of habitat resulted in high abundances of northern pike in the chain lakes and Coeur d'Alene Lake. Northern pike quickly became a very popular sport fish due to their novelty, abundance, and ability to reach a large size. The Idaho Department of Fish and Game introduced smallmouth bass to Idaho in 1905. Smallmouth bass were introduced in response to angler interest and for their ability to occupy cool and coldwater habitats common throughout the state (Simpson and Wallace 1982, Dillon 1992). Smallmouth bass were transported to additional water bodies by anglers. For example, smallmouth bass are thought to have been illegally introduced to Coeur d'Alene Lake from Hayden Lake in the early 1990s (Anders et al. 2003).

Understanding the population dynamics of nonnative species is important to guide management actions regardless how they entered the system. Unfortunately, the population demographics and dynamics of northern pike and smallmouth bass in Coeur d'Alene Lake have not been thoroughly studied. This lack of knowledge limits the ability of managers to make informed decisions. Thus, the objective of this study was to describe the population demographics and dynamics of northern pike and smallmouth bass in Coeur d'Alene Lake, Idaho. Additionally, growth data were compared to other northern pike and smallmouth bass populations across their distributions to place the growth of these two nonnative species in the context of other populations and help discern large-scale patterns.

Methods

Coeur d'Alene Lake is the second largest natural lake in Idaho with a surface area of 12,700 ha (Figure 1). The lake has a mean depth of approximately 24 m and a maximum depth of 61 m (Rich 1992, Vitale et al. 2004). Primary tributaries to Coeur d'Alene Lake are the Coeur d'Alene and St. Joe rivers, with many small streams also contributing to the system. Post Falls Dam was constructed on the outlet in 1906 and raised the water level of the lake by 2.5 m creating an abundance of shallow, vegetated habitat (Rich 1992). The lake has been classified as mesotrophic based on nutrient concentrations; however, heavy metals from 100 years of mining and ore processing in the

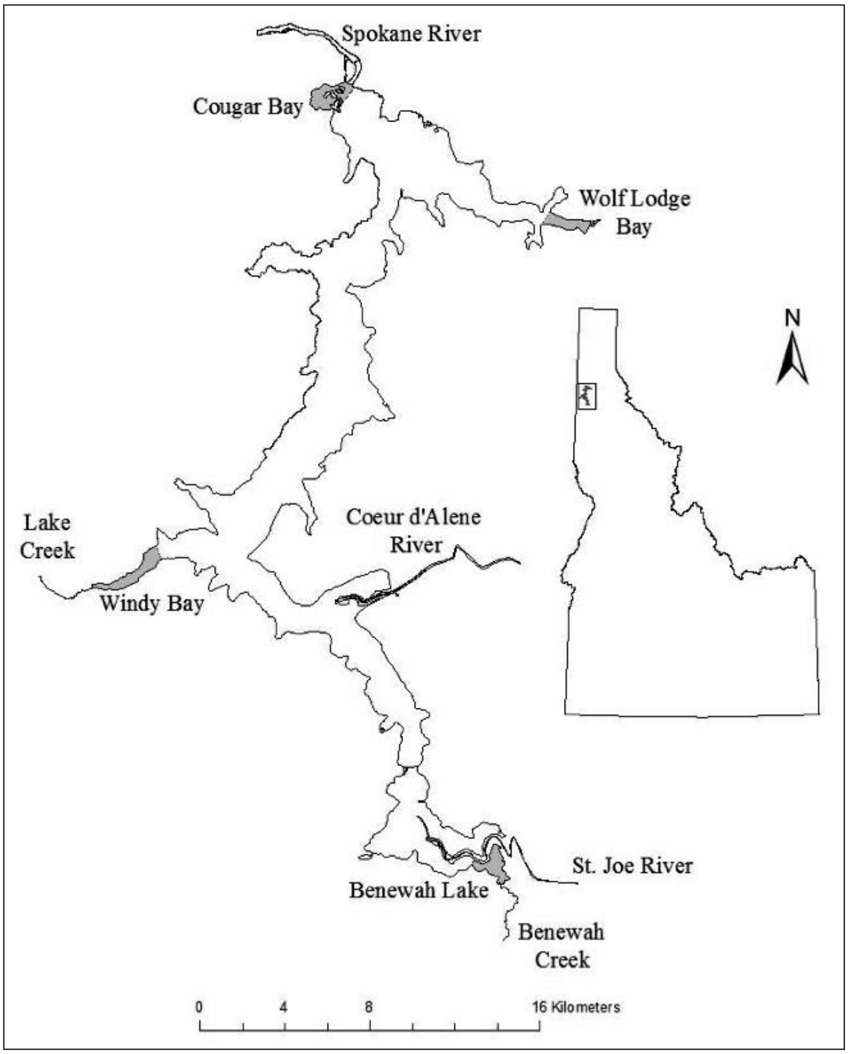

Figure 1. Map of Coeur d'Alene Lake in northern Idaho. Idaho Department of Fish and Game manages the lake north of the mouth of the Coeur d'Alene River. The Coeur d'Alene Tribe manages the lake south of the mouth of the Coeur d'Alene River as well as the Lake Creek watershed. Sampling sites were located in Cougar, Wolf Lodge, and Windy bays, and Benewah Lake.

watershed limit biological production (Committee on Superfund Site Assessment Remediation in the Coeur d'Alene River Basin National Research Council 2005).

Study sites in Coeur d'Alene Lake included Wolf Lodge, Cougar, and Windy bays and Benewah Lake (Figure 1). These locations were selected because they support populations of northern pike and smallmouth bass and are important areas for sport-fish management. The shorelines of the four bays were divided into 300 m sections and stratified random sampling was used to randomly assign a section to a gear. A sampling event consisted of sampling eighteen non-overlapping sections (i.e., 12 gill net and 6 electrofishing sites). A sampling event occurred once per month in Cougar and Wolf Lodge bays from March 2012 to May 2013. Windy Bay and Benewah Lake were sampled once per month from June to November of 2012 and twice per month from March to May of 2012 and 2013. Hazardous lake conditions prevented sampling during winter (i.e., December 2012–February 2013).

Electrofishing and gill netting were used to maximize catch of northern pike and smallmouth bass. Pulsed-DC electrofishing was conducted using a 5,000 W generator mounted in an aluminum boat with Smith-Root (Smith-Root, Inc., Vancouver, Washington) equipment. Power output was standardized to 2,750–3,250 W based on ambient water conductivity (μS/cm; Miranda and Boxrucker 2009). Experimental gill nets (46 m × 1.8 m with panels of 25, 32, 38, 44, 50-mm bar-measure mesh) were fished for 1.5–2.0 hours to minimize mortality. Kobler et al. (2008) found that northern pike movement was more homogenous during the winter than in other months, with higher movement occurring during the day. Thus, nets were set at dusk, except during October–April when nets were fished during the day. Additionally, operating a boat at night during periods with low water (e.g., fall, winter) was hazardous due to ice and the emergence of obstacles (e.g., logs, islands).

Total length from northern pike and smallmouth bass was measured to the nearest millimeter and weight was recorded to the nearest gram. Nonlethal age structures, including dorsal spines from smallmouth bass and pelvic fin rays from northern pike, were collected from ten fish per centimeter length group (Laine et al. 1991, Quist et al. 2012). Spines and fin rays were placed into coin envelopes and allowed to air dry before processing (Koch and Quist 2007). Otoliths from smallmouth bass and cleithra from northern pike were collected from mortalities to corroborate ages from pelvic fin rays and dorsal spines. Agreement between ages for otoliths and dorsal spines from smallmouth bass was 100%. Similarly, age agreement was 100% between cleithra and fin rays from northern pike.

Half of the captured northern pike were tagged using an individually-numbered, non-reward FD-94 T-bar anchor tag (76 mm; Floy Tag Inc., Seattle, Washington) that was inserted near the posterior end of the dorsal fin. All other northern pike were tagged with an individually-numbered, non-reward 6 mm × 16 mm Carlin dangler tag (Floy Tag Inc., Seattle, Washington) that was inserted in the caudal peduncle (Quist et al. 2010). Tag loss was assessed on all northern pike by completely removing the left pelvic fin (Nielson 1992, Guy et al. 1996). All tags also had the telephone number for the Idaho Department of Fish and Game's tag-reporting hotline. Smallmouth bass exploitation was reported to be low from a creel survey performed by the Idaho Department of Fish and Game (Hardy et al. 2009). Therefore, smallmouth bass were only marked by completely removing the left pelvic fin (Nielson 1992, Guy et al. 1996).

Proportional size distribution (PSD) was estimated to describe the length structure of northern pike and smallmouth populations:

$$PSD = \left(\frac{a}{b}\right) \times 100,$$

where a equals the number of fish with a total length greater than or equal to the minimum length category and b is the number of fish with a total length greater than or equal to the minimum stock length (Neumann et al. 2012). Size structure indices provide a numerical description of length-frequency data that can be used to gain insight about fish population dynamics. Length-frequency distributions were summarized with PSDs for both northern pike and smallmouth bass for quality (northern pike = 530 mm; smallmouth bass = 280 mm), preferred (710 mm; 350 mm), and memorable (860 mm; 430 mm) length categories. Minimum total lengths for length categories were provided by Neumann et al. (2012).

The interaction between fishing and natural mortality is highly complex, and disentangling their separate effects is difficult. Consequently, total annual mortality is most commonly used to evaluate mortality of fishes, particularly across large geographic areas. Total annual mortality was estimated from age-3 and older northern pike and age-2 and older smallmouth bass using a weighted catch curve of $\log_e$(number of fish) as a function of age (Miranda and Bettoli 2007, Smith et al. 2012). Younger individuals were excluded from the analysis as they were not fully recruited to the sampling gears. Gillnetting data for northern pike and electrofishing data for smallmouth bass were used for the catch curve analysis. Recruitment variation was measured using the coefficient of determination (r^2; recruitment coefficient of determination [RCD]) from a simple linear regression of $\log_e$(number of fish) as a function of age (Isermann et al. 2002). The RCD varies from -1 to 1; values approaching 1 indicate stable recruitment (Isermann et al. 2002). Exploitation for northern pike was estimated using the non-reward tag reporting rate (54.2%) described by Meyer et al. (2012) along with our estimates of tag loss (10.2%) and tagging mortality (0.4%).

Back-calculated lengths-at-age were estimated using the Dahl-Lea method:

$$L_i = \frac{S_i}{S_c} \times L_c$$

where L_i is the back-calculated length of the fish when the ith increment was formed, L_c is length of the fish at capture, S_c is the radius of the ageing structure at capture, and S_i is the radius of the ageing structure at the ith increment (Quist et al. 2012). Mean back-calculated lengths-at-age for northern pike and smallmouth bass were summarized by bay and for the lake. In addition, a von Bertalanffy growth model was fit for northern pike and smallmouth bass populations in Coeur d'Alene Lake:

$$L_t = L_\infty \times (1 - e^{-K(t-t_0)}),$$

where L_t is the length at time t, L_∞ is the theoretical maximum length, K is the Brody growth coefficient, and t_0 is the time when length would theoretically equal 0 mm. Growth estimates of northern pike and smallmouth bass in Coeur d'Alene Lake were compared to North America percentiles (i.e, 5th, 25th, 50th, 75th, and 95th) of mean lengths-at-age of fish from lentic systems (Bonar et al. 2009).

Nonmetric multidimensional scaling (NMDS) was used to examine how growth and longevity of northern pike and smallmouth bass in Coeur d'Alene Lake compared to other populations on a large-scale (Kruskal and Wish 1984). Data used for NMDS analysis were gleaned from published literature across northern pike and smallmouth bass distributions from lentic systems. Growth data used for the NMDS analysis consisted of K and L_∞ from the von Bertalanffy growth model, maximum age, and length-at-age 3. Northern pike and smallmouth bass growth data were grouped into regions. Regions used for northern pike included north-central United States (i.e., Iowa, Minnesota, South Dakota and Wisconsin), northeast United States (i.e., New York and Ohio), Ontario, Northwest Territories, and Europe (i.e., Croatia, England, Lithuania, Ireland, Italy and Scotland). Smallmouth bass regions were divided into the northwest United States (i.e., Idaho and Washington), north-central United States (i.e., Illinois, Wisconsin and Great Lakes), northeast United States (i.e., Maryland, Massachusetts, New York, Pennsylvania and Virginia), southwest United States (i.e., Southern California), south-central United States (i.e., Oklahoma and Texas), and southeast United States (i.e., North Carolina and Tennessee). The NMDS ordinations were conducted using Bray-Curtis dissimilarity measures in the Vegan package, Program R (R Development Core Team 2009).

Results

A total of 736 northern pike was captured, of which 573 were marked and 98 were recaptured. The proportion of recaptures of northern pike was highest (38%) in Windy Bay, whereas the proportion of recaptures in other bays was roughly 9% (Table 1). A total of 1,418 smallmouth bass was also sampled, of which 772 were marked and 19 were recaptured. Smallmouth bass recaptures were rare (~2%) in Wolf Lodge, Cougar, and Windy bays and none were recaptured in Benewah Lake (Table 1). Electrofishing captured 58 northern pike and 678 were sampled with gill netting. Electrofishing catch rates for northern pike were generally low, but were highest in the fall (Figure 2). Northern pike catch rates using gill nets were highest in the spring and decreased by about 50% in the summer and fall (Figure 2). Electrofishing captured 1,316 smallmouth bass and 102 smallmouth bass were sampled with gill netting. Catch rates for smallmouth bass were consistently high in Wolf Lodge Bay and low in Benewah Lake across all seasons (Figure 2). Catch rates of smallmouth bass using gill nets were relatively low for all seasons (Figure 2). In total, 566 northern pike varying from 162 to 1080 mm were tagged. Anglers reported 93 tags

TABLE 1. Frequency of northern pike and smallmouth bass marked or recaptured using standard sampling gears in bays in Coeur d'Alene Lake, Idaho.

	Northern pike		Smallmouth bass	
Site	# marked (%)	# recaptured (%)	# marked (%)	# recaptured (%)
Wolf Lodge Bay	44 (8)	3 (3)	372 (48)	11 (58)
Cougar Bay	85 (15)	7 (7)	57 (7)	1 (5)
Windy Bay	143 (25)	55 (56)	337 (44)	7 (37)
Benewah Lake	301 (52)	33 (34)	6 (1)	0 (0)
All sites	573 (100)	98 (100)	772 (100)	19 (100)

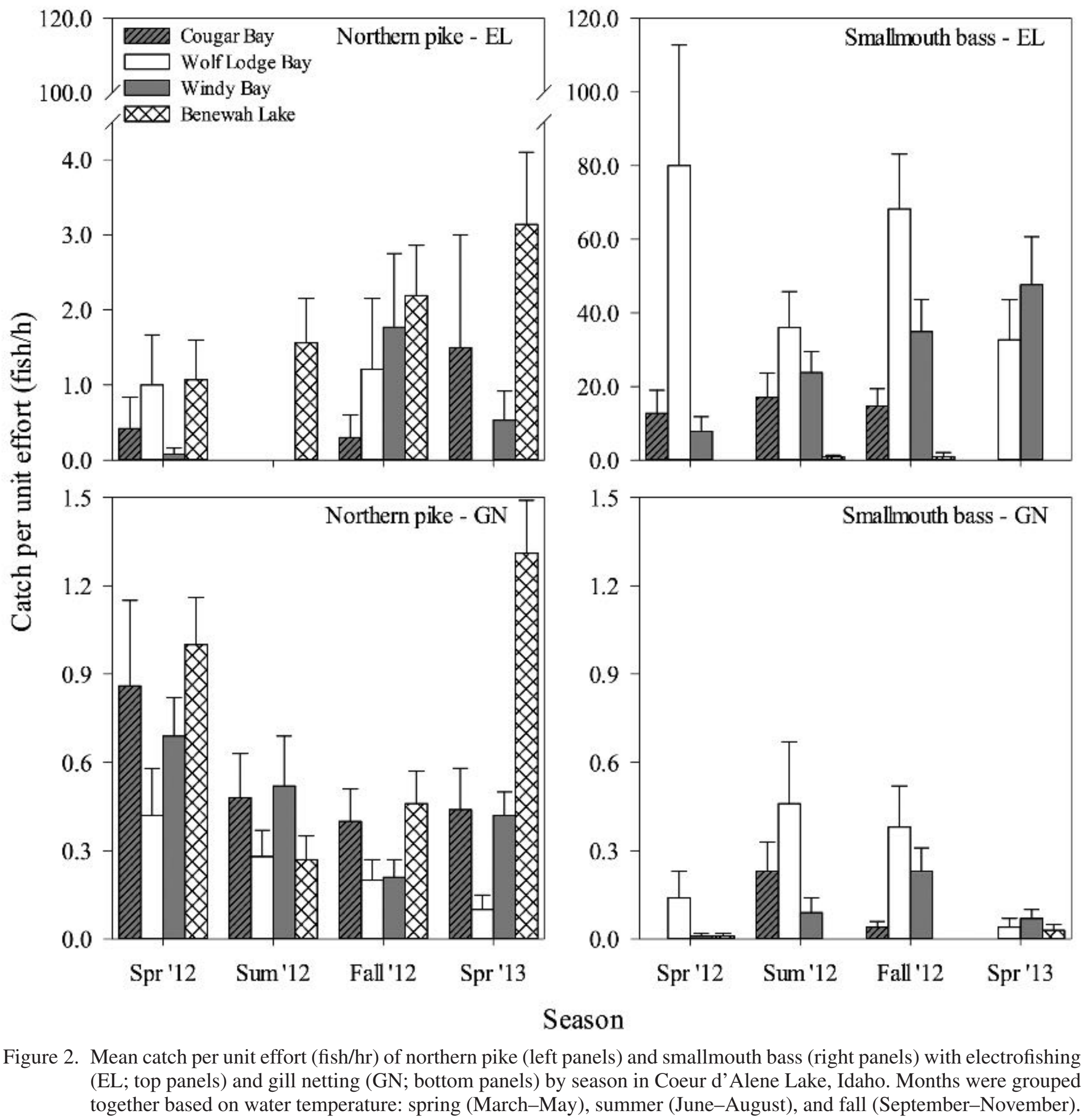

Figure 2. Mean catch per unit effort (fish/hr) of northern pike (left panels) and smallmouth bass (right panels) with electrofishing (EL; top panels) and gill netting (GN; bottom panels) by season in Coeur d'Alene Lake, Idaho. Months were grouped together based on water temperature: spring (March–May), summer (June–August), and fall (September–November). Error bars represent one standard error.

to the Idaho Department of Fish and Game. Of the fish caught and reported, 48 (51.6%) of the fish were captured during spring. Seventy-nine of the reported fish (85.0%) were harvested. Exploitation of northern pike was estimated at 31.0%.

Size structure of northern pike was similar across all bays with slightly smaller fish in Benewah Lake (Figure 3). Proportional size distribution of preferred-length northern pike was highest in Windy Bay. Similar to northern pike, the PSD for smallmouth bass was similar in each bay with smaller fish in Windy Bay (Figure 4). The smaller size structure of smallmouth bass in Windy Bay was made more evident by the lower PSD-P and PSD-M values. Smallmouth bass PSD-P and PSD-M for Benewah Lake were not calculated as individuals greater than or equal to 280 mm (i.e., quality-length fish) were not captured. The RCD was 0.99 for northern pike and 0.98 for smallmouth bass, indicating highly stable recruitment (Figure 5). Total annual mortality was estimated as 66% for northern pike and 42% for smallmouth bass (Figure 5).

Growth of northern pike was similar across all bays with the exception of Wolf Lodge Bay, where growth began to slow at age 3 (Figure 6). Growth of northern pike in Coeur d'Alene Lake was between the 50th and 75th percentiles for North America lentic populations (Figure 7). Growth of smallmouth bass in Windy and Wolf Lodge bays was similar for all ages (Figure 6). Mean length-at-age of smallmouth bass was generally highest in Cougar Bay. Mean length-at-age of smallmouth bass in Benewah Lake was not calculated due to small sample sizes. Smallmouth bass in Coeur d'Alene Lake grew extremely slow and was most similar to populations in the 5th percentile for North America (Figure 7).

The NMDS analysis of growth from lake systems produced stable ordinations for northern pike (2 axes; stress = 0.03; Figure 8) and smallmouth bass (2 axes; stress = 0.04; Figure 9). Northern pike populations clustered into four groups (e.g., Ontario, Northwest Territories, Europe and northern United States). Growth of northern pike in Coeur d'Alene Lake was most similar to populations in the north-central and northeast United States with fast growth rates and short life spans. The NMDS ordination of growth for smallmouth bass was highly variable between regions and clustered into north and south groups. Smallmouth bass growth in Coeur d'Alene Lake was similar to other populations in northern regions of the United States displaying slow growth rates with high longevity.

Discussion

The results of this study provide natural resource managers with important information on the population demographics and dynamics of two important nonnative sport fish species: northern pike and smallmouth bass. The majority of northern pike obtained lengths of quality length (530 mm) or longer in each bay at young ages suggesting fast growth. Interestingly, Rich (1992) also reported that the PSD of northern pike in Cougar Bay was 94 and hypothesized that the size structure would decrease due to increased angler interest and high exploitation. Twenty years later, PSDs near 90 were observed throughout the Coeur d'Alene system. Size structure of smallmouth bass was similar between bays with the majority of individuals less than stock length (180 mm). Low PSDs are generally indicative of slow growth or high mortality of large fish (Anderson and Weithman 1978). Smallmouth bass in Coeur d'Alene Lake do not reach quality length (i.e., 280 mm) until age 7, suggesting that slow growth is at least partly responsible for the low PSDs.

Estimates of total annual mortality for northern pike and smallmouth bass vary greatly across their distributions. Kempinger and Carline (1978) reported high total annual mortality rates for northern pike varying from 59% to 91% in Escanaba Lake, Wisconsin. Alternatively, low total annual mortality rates varying from 19% to 57% were reported by Mosindy et al. (1987) for Savanne Lake, Ontario and by Diana (1983) for three Michigan lakes. Total annual mortality for northern pike in Coeur d'Alene Lake was relatively high (i.e., 66%). Total annual mortality of smallmouth bass was lower (i.e., 42%) than those reported for other systems in the Pacific Northwest. For example, Anglea (1997) reported that total annual mortality was 52% for smallmouth bass in Lower Granite Reservoir, Washington. Beamesderfer and North

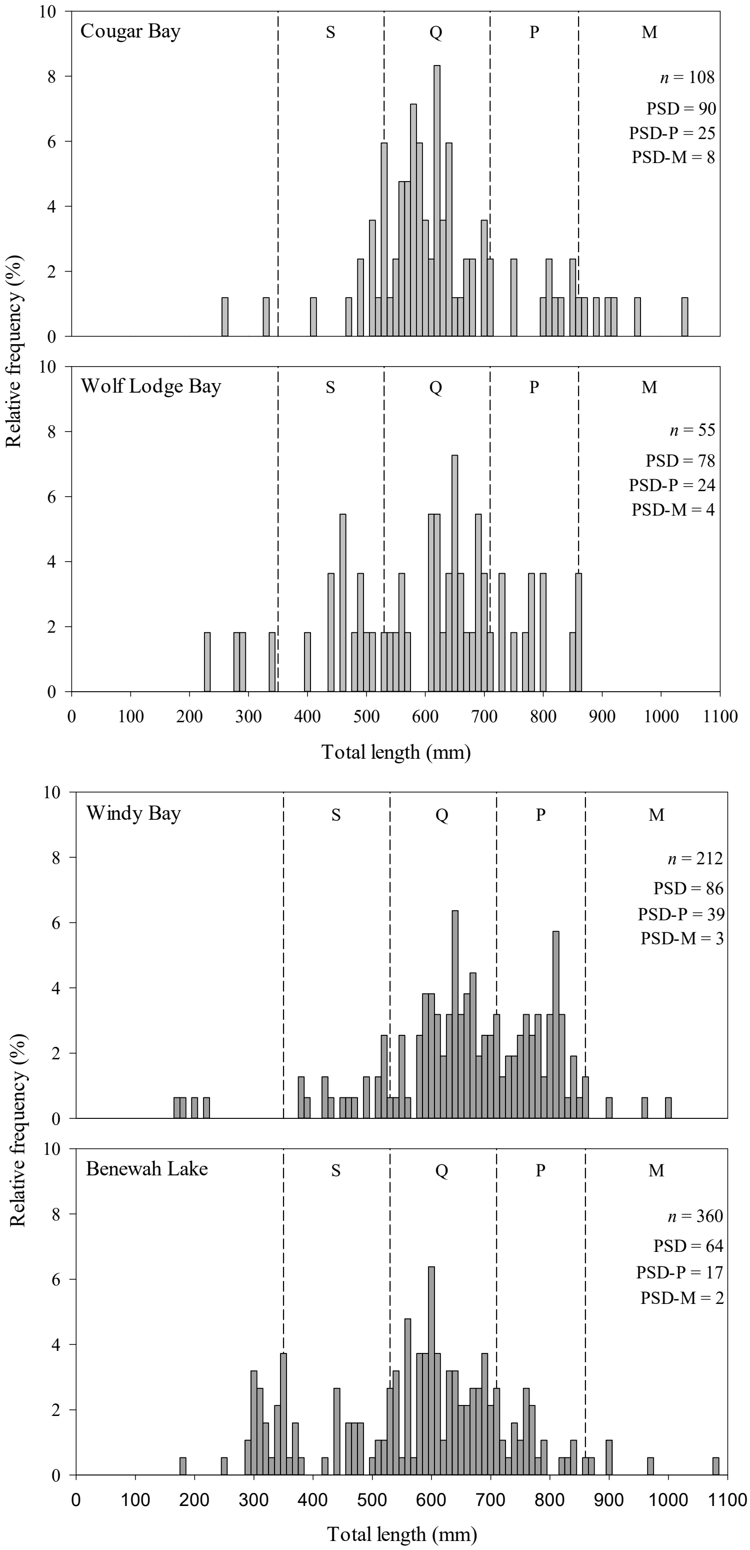

Figure 3. Length-frequency distribution, sample size, proportional size distribution (PSD), PSD of preferred-length fish (PSD-P), and PSD of memorable-length fish (PSD-M) for northern pike in Cougar, Wolf Lodge, and Windy bays, and Benewah Lake in Coeur d'Alene Lake, Idaho. Dashed lines represent boundaries for stock (S), quality (Q), preferred (P), and memorable (M) length categories.

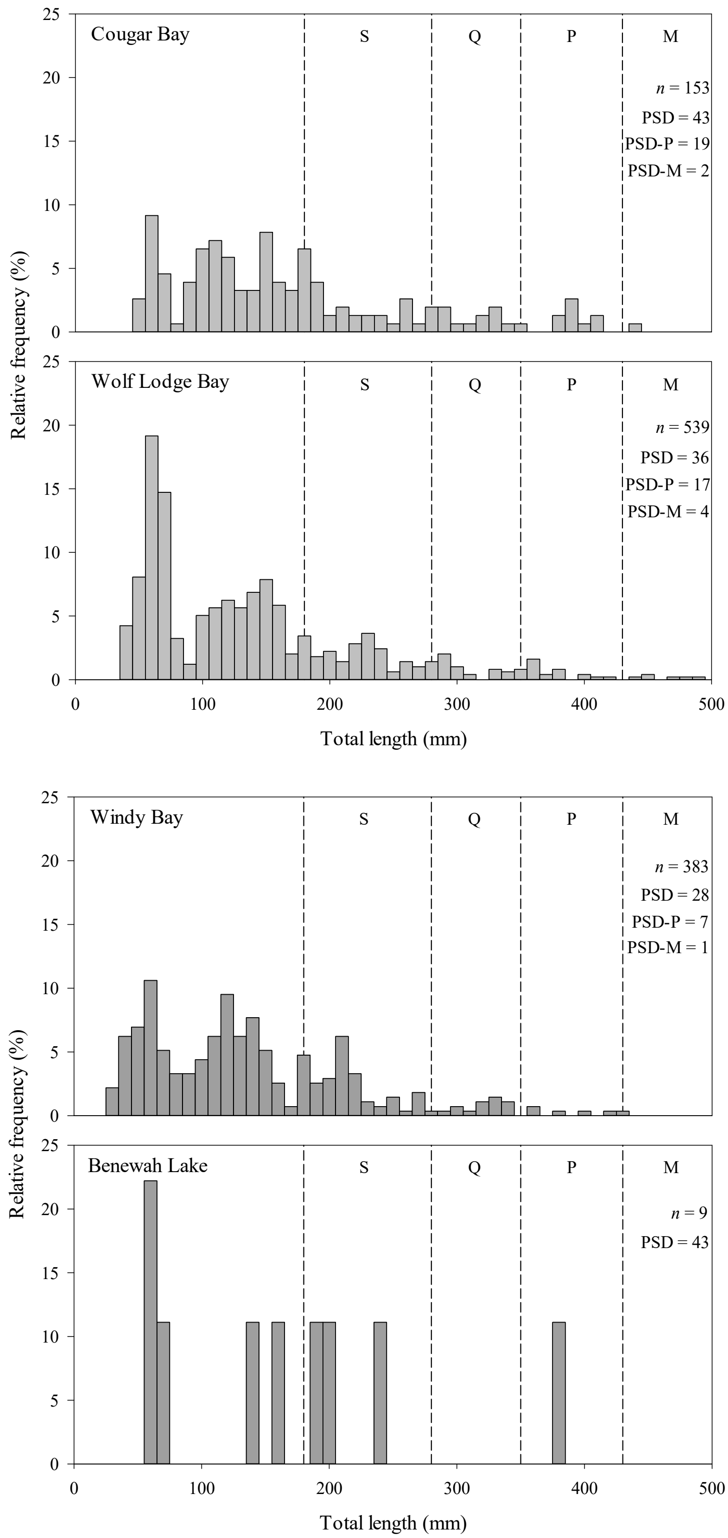

Figure 4. Length-frequency distribution, sample size, proportional size distribution (PSD), PSD of preferred-length fish (PSD-P), and PSD of memorable-length fish (PSD-M) for smallmouth bass in Cougar, Wolf Lodge, and Windy bays, and Benewah Lake in Coeur d'Alene Lake, Idaho. Dashed lines represent boundaries for stock (S), quality (Q), preferred (P), and memorable (M) length categories.

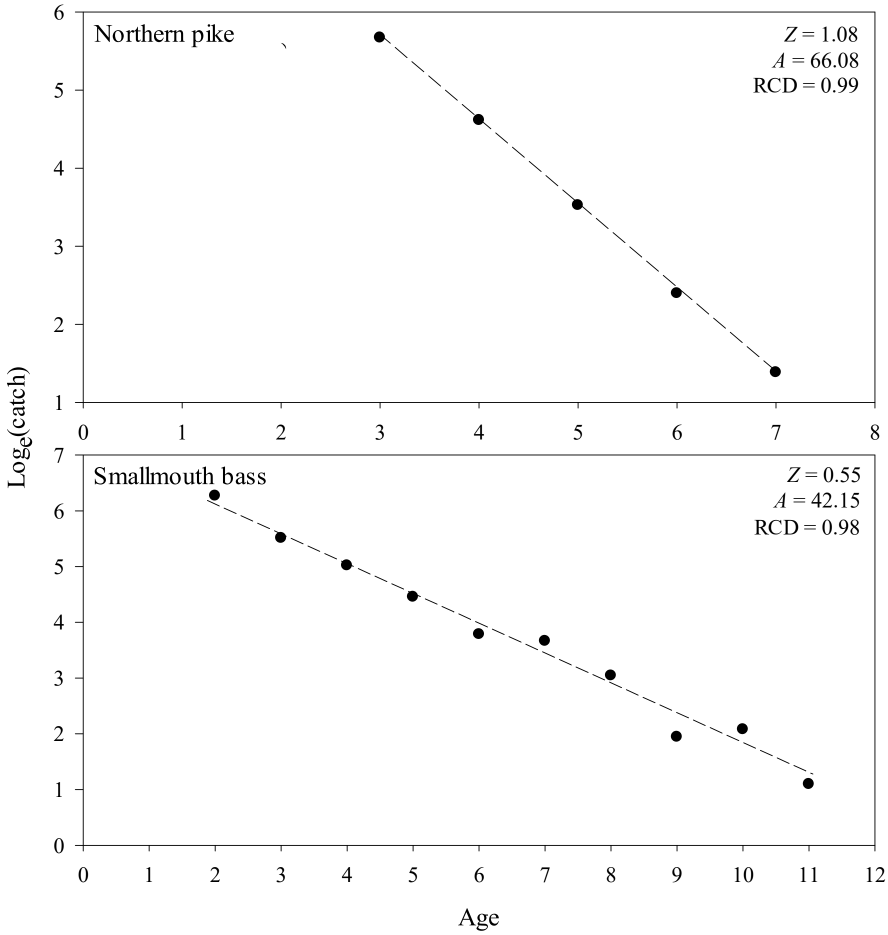

Figure 5. Instantaneous (*Z*) total mortality, total annual mortality % (*A*), and recruitment coefficient of determination (RCD) for northern pike (top panel) and smallmouth bass (bottom panel) in Coeur d'Alene Lake, Idaho.

(1995) reported that growth and mortality rates of smallmouth bass were lower in waters in northern latitudes, but also noted that smallmouth bass in unproductive northern waters could display slow growth and high mortality.

Exploitation of northern pike was moderately high (31%) with the majority of fish caught during spring. Few tags were reported during the summer, likely due to northern pike inactivity and individual fish moving to deeper water after spawning (Diana et al. 1977, Rosell and MacOscar 2002). A noticeable decrease in the number of tags returned for northern pike after spring is also likely a result of anglers seeking other nonnative sport fish species such as largemouth bass *Micropterus salmoides*, Chinook salmon *Oncorhynchus tshawyscha*, and kokanee *O. nerka*. The primary drivers for mortality of smallmouth bass are also difficult to identify. Dunlop et al. (2005) argued that higher mortality of smallmouth bass in Provoking Lake, Ontario relative to Opeongo Lake, Ontario was due to resource limitations. Similar mechanisms may be regulating survival of smallmouth bass in Coeur d'Alene Lake.

Growth is often used as an indication of resource availability. Fast growth rates are often common for populations with abundant food resources and quality habitat (Allen and Hightower 2010).

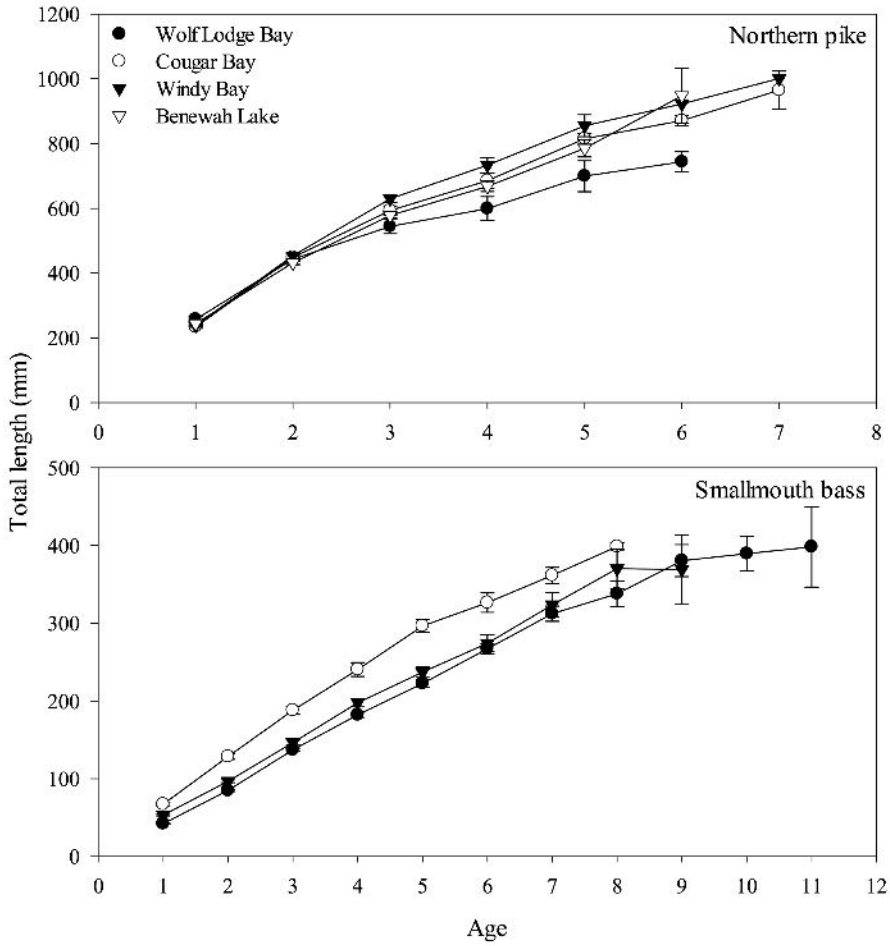

Figure 6. Mean back-calculated length-at-age for northern pike (top panel) and smallmouth bass (bottom panel) in bays sampled in Coeur d'Alene Lake, Idaho. Mean back-calculated length-at-age could not be derived in Benewah Lake for smallmouth bass due to the small sample size. Error bars represent one standard error.

Alternatively, slow growth rates often indicate that fish densities are too high for available resources (Allen and Hightower 2010). Rich (1992) reported that lengths of northern pike from Cougar Bay were 31% higher than the North American average reported by Carlander (1969). Rich (1992) also found the oldest individual was age 8 and noted that the rapid growth rate was likely limiting longevity. We showed similar growth rates and age structure of northern pike. Age-1 to age-4 northern pike had growth rates that were similar to the 50th percentile of North American populations (Bonar et al. 2009). Individuals older than age 4 approached the 75th percentile. In contrast to northern pike, growth of smallmouth bass in Coeur d'Alene Lake was extremely slow compared to other smallmouth bass populations in North America (Bonar et al. 2009). Similarly, Anglea (1997) reported smallmouth bass in Lower Granite Reservoir, Washington grew slowly (~25th percentile of North America populations).

The rates of growth and mortality observed for northern pike and smallmouth bass in our study could be explained by latitudinal patterns in fish population dynamics that have been well documented for other species (Quist et al 2003, Denit

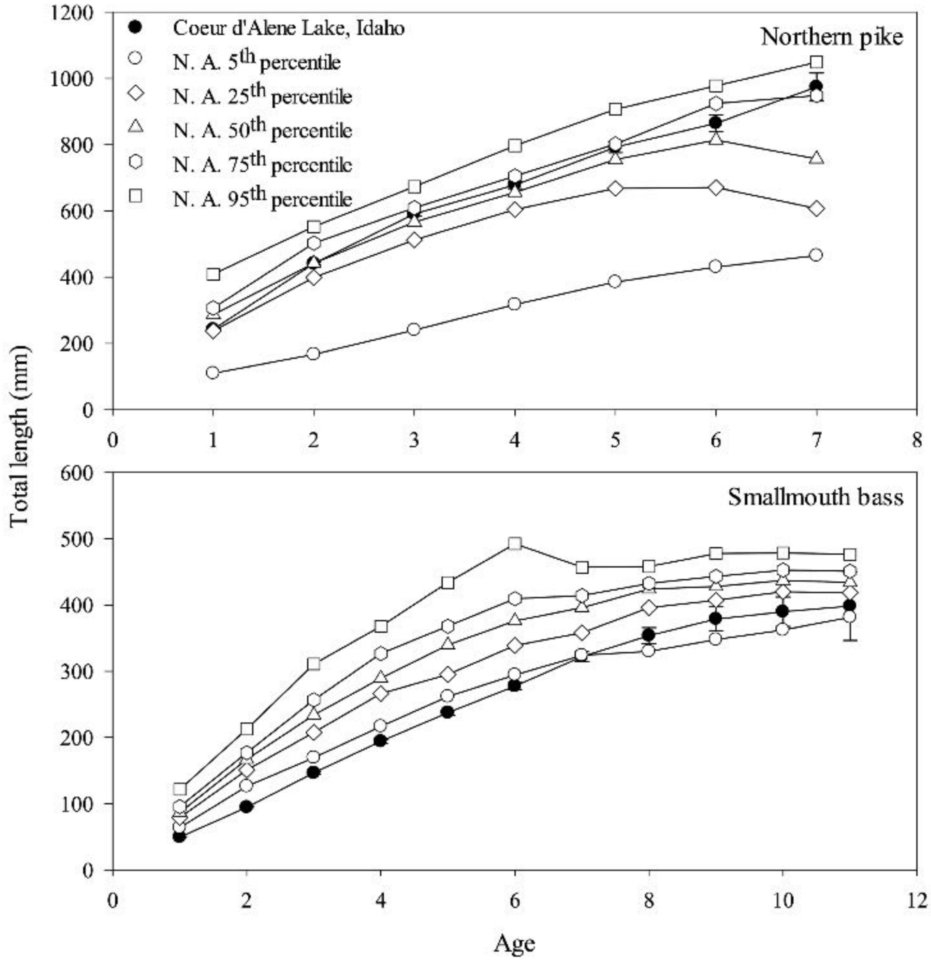

Figure 7. Mean back-calculated length-at-age for northern pike (top panel) and smallmouth bass (bottom panel) in Coeur d'Alene Lake, Idaho compared to North America (N. A.) lentic percentiles. Error bars represent one standard error.

and Sponaugle 2004). Populations in northern latitudes often exhibit slower growth rates, greater longevity, and lower total annual mortality than southern latitudes (Beverton 1987, Quist et al. 2003, Porter et al. 2014). Several mechanisms are likely related to these latitudinal patterns. Studies have shown that fishes in northern latitudes will often invest more energy into somatic growth and delay reproduction, whereas those at southern latitudes will reproduce at a younger age and smaller size (Heibo et al. 2005, Blanck and Lamouroux 2007). Braaten and Guy (2002) reported that increases in water temperature, degree-days, and the duration of the growing season from north to south were related to increased growth of numerous fishes in the Missouri and lower Yellowstone rivers. Rypel (2012) stated annual growth rates of northern pike in North America were primarily driven by water temperature and decreased with increasing latitude. Similar mechanisms are likely responsible for the large-scale patterns in growth we observed for northern pike and smallmouth bass populations. Northern pike in northern latitudes (i.e., Northwest Territories) grew at slower rates with greater longevity compared to the Coeur d'Alene Lake population; Coeur d'Alene Lake

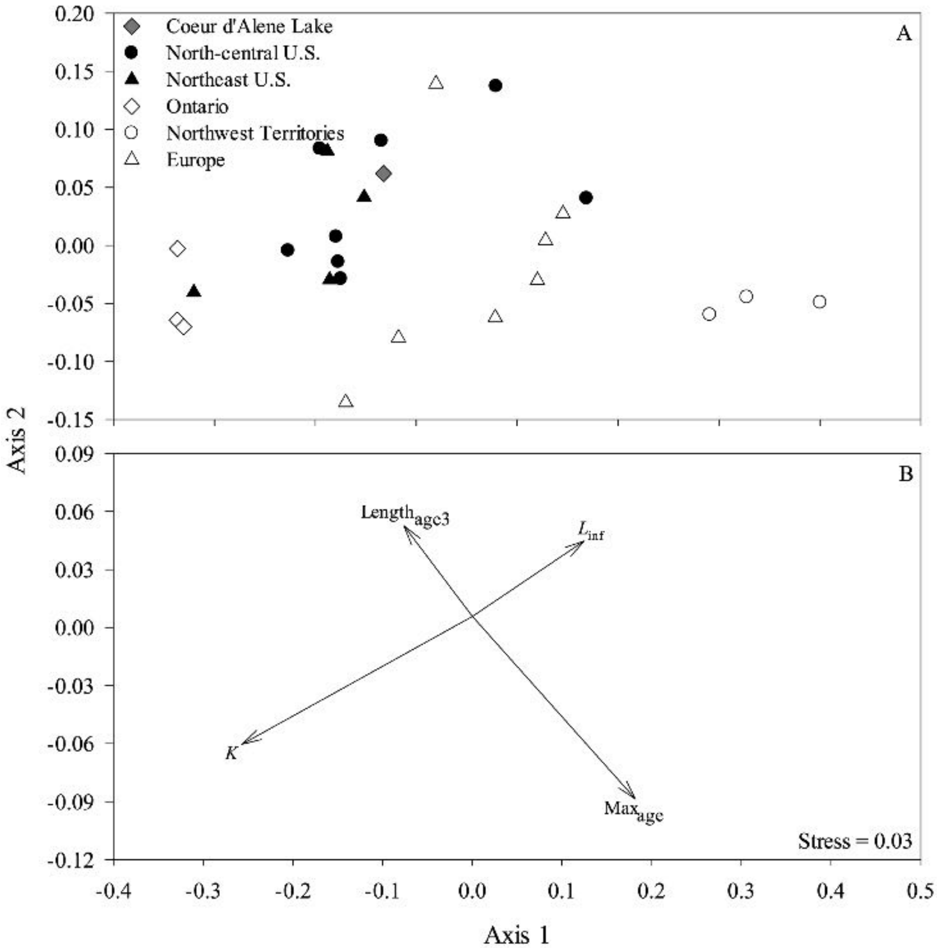

Figure 8. Nonmetric multidimensional scaling (NMDS) ordination of growth (A) from 27 lentic northern pike populations from across their circumpolar distribution. Vectors (B) indicate directions and strength of correlations within the NMDS ordination. Growth vectors were the growth coefficient (K), the theoretical maximum length (L_{inf}), maximum age (Max$_{age}$), and the mean length-at-age three (Length$_{age3}$).

is near the southern end of their circumpolar distribution. Similarly, smallmouth bass at southern latitudes grew at faster rates and had lower longevity compared to northern populations such as Coeur d'Alene Lake. Acknowledging latitudinal differences in population dynamics can result in better management of sport-fish populations and provides a broader context for understanding population dynamics.

Growth of individuals can be influenced by many other factors such as inter- and intraspecific competition, food availability, physiological demands, and temperature (Weatherley 1976). We are unable to identify the primary driver for the high growth rate of northern pike in Coeur d'Alene Lake. However, high mortality and abundant prey fishes likely prompted their fast growth. In relation to the slow growth of smallmouth bass, the Coeur d'Alene basin has a long history of mining that has resulted in a significant reduction in the productivity of invertebrates in Coeur d'Alene Lake (Savage and Rabe 1973). Dunlop et al.

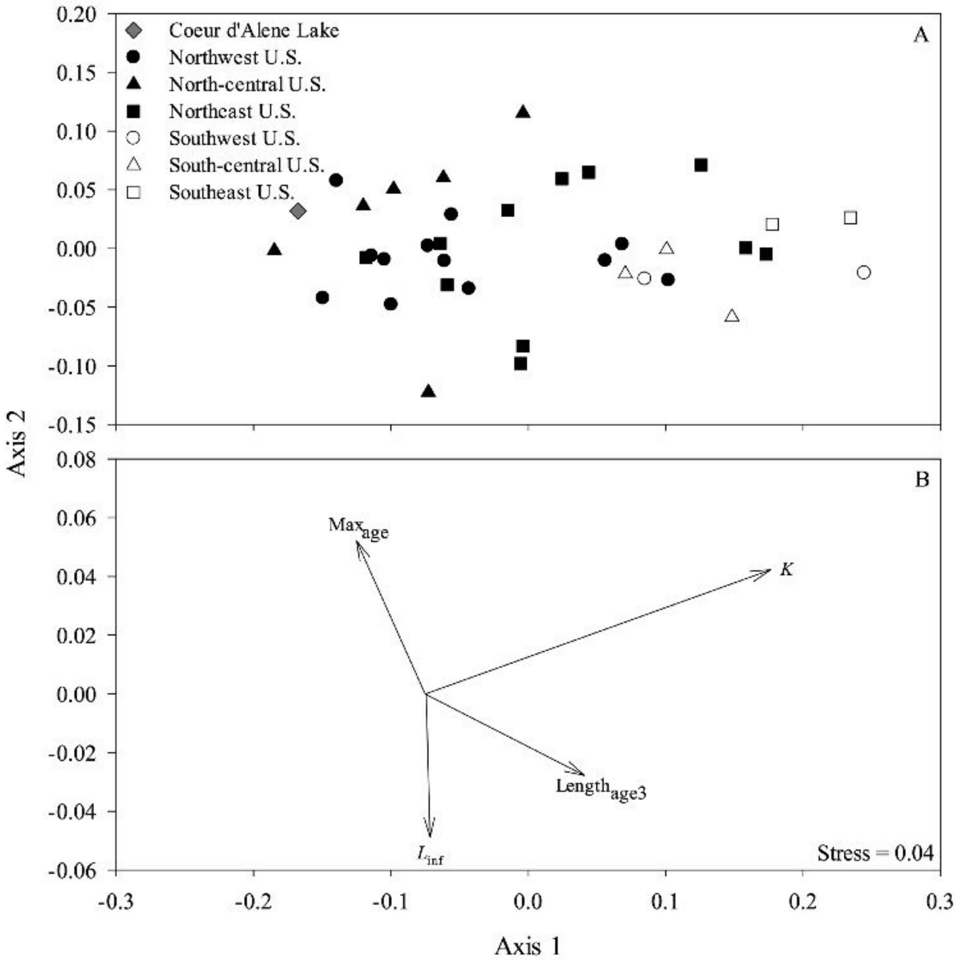

Figure 9. Nonmetric multidimensional scaling (NMDS) ordination of growth (A) from 37 lentic smallmouth bass populations. Vectors (B) indicate directions and strength of correlations within the NMDS ordination. Growth vectors were the growth coefficient (*K*), the theoretical maximum length (L_{inf}), maximum age (Max_{age}), and the mean length-at-age three ($Length_{age3}$).

(2005) suggested that intraspecific competition of smallmouth bass was a primary factor for slow growth in Provoking Lake, Ontario. Similarly, low invertebrate productivity of Coeur d'Alene Lake coupled with intraspecific competition could explain the slow growth of smallmouth bass in the system.

The population dynamics were dissimilar for the two nonnative species examined in this study. Northern pike in Coeur d'Alene Lake exhibited fast growth with a large proportion being greater than quality length (710mm), likely due to high mortality and low density. Stable recruitment of northern pike in Coeur d'Alene Lake indicated that density-dependent effects likely influenced year classes similarly. Alternatively, smallmouth bass grew slowly with a large proportion of the population being less than stock length (180mm), likely due to low availability of invertebrates and intraspecific competition. Smallmouth bass in Coeur d'Alene Lake also displayed stable recruitment suggesting that density-dependent factors probably influenced their year classes similarly. The description of the population dynamics and their potential drivers for these two nonnative species provides important insight on their ecology and management.

Acknowledgments

We thank C. Brown, M. Castaneda, W. Field, B. Harper, E. Hendrickson, J. Fredericks, D. Jolibois, I. Lee, N. Porter, J. Sanchez, T. Schill, C. Smith, J. Smith, M. Stanger, C. Watkins, S. Whitlock, and T. Wilson for assistance with field research. We also thank A. Vitale from the Coeur d'Alene Tribe and J. Fredricks from the Idaho Department of Fish and Game for assistance in planning and implementing this study. We also thank S. Elle, D. Jensen, L. Mamer, and K. Stevenson from the Idaho Department of Fish and Game. K. Pope, M. Wiest, F. Wilhelm, and two anonymous reviewers provided helpful comments on an earlier version of this manuscript. Funding for the project was provided by the Coeur d'Alene Tribe. Additional support was provided by the U.S. Geological Survey and Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, Idaho Department of Fish and Game, Coeur d'Alene Tribe, and Wildlife Management Institute. This project was conducted under the University of Idaho Institutional Animal Care and Use Committee Protocol 2011-43. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Received 7 March 2014

Accepted for publication 23 January 2015

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