Walleye (*Sander vitreus*)

An Overview of Invasion With an Emphasis on the Pacific Northwest

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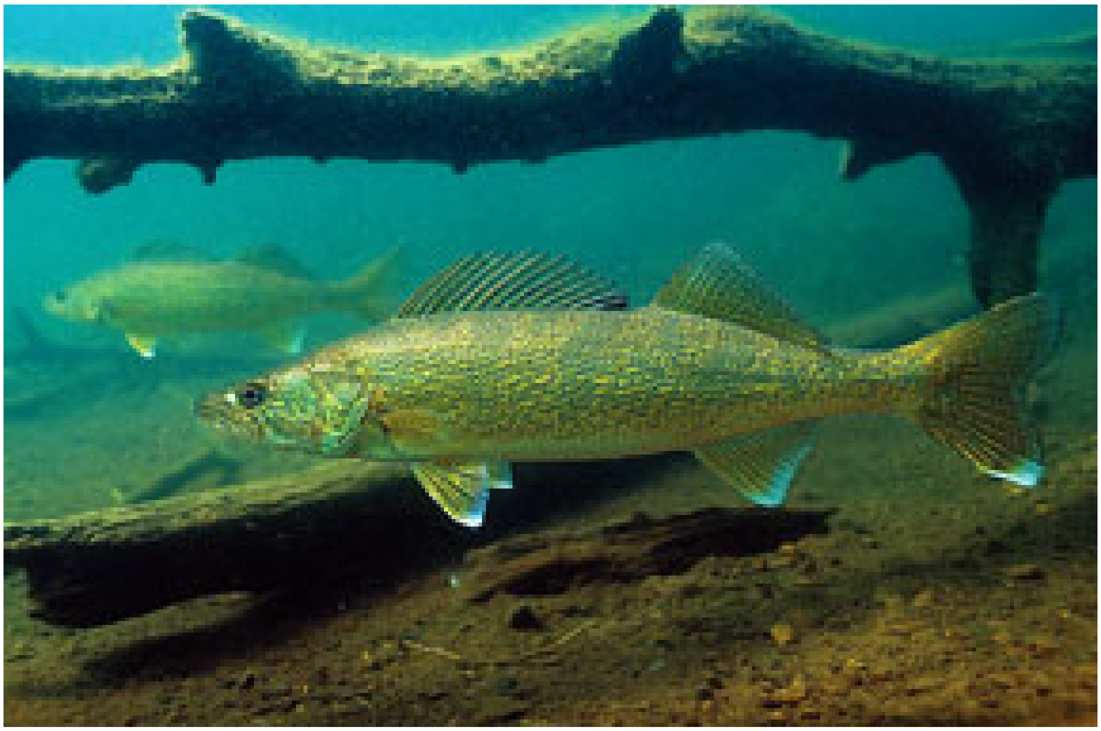

Diagnostic Information

Common Names: Walleye, walleyed pike, blue pike, jack, yellow walleye

Order: Perciformes

Family: Percidae

Genus: *Sander*

Species: *vitreus*

Formerly classified as *Stizostedion vitreum*, the scientific name for walleye was changed to *Sander vitreus* in 2003 (Nelson et al. 2003). Walleye have an elongate, subcylindrical body that becomes more compressed with age (Scott and Crossman 1973). The body can range from olive-brown to golden-brown to yellow in color, with the ventral surface ranging from yellow to white (Craig 2000). Other distinguishing characteristics of walleye include 2 spines in the anal fin, 2 distinct dorsal fins with a dark spot at the base of the first dorsal, as well as a large terminal mouth with prominent canine teeth (Wydoski and Whitney 1979). Additionally, their eyes are highly reflective and appear silvery (Craig 2000). The average length for a mature adult is approximately 330-500 mm (Scott and Crossman 1973), although they can grow much larger, with the current IGFA world record measuring 1041 mm and weighing 11.3 kg.

In the Pacific Northwest, walleye may be confused with fellow Percids, yellow perch (*Perca flavescens*) and sauger (*Sander Canadensis*). Walleye can be distinguished from yellow perch by the presence of canine teeth, 12-13 anal fin rays (yellow perch have 6-8), and a lack of dark vertical bars on the sides of the body (Wyodoski and Whitney 1979). Although they only exist sympatrically in one location in the Pacific Northwest (Bear River Drainage, Idaho) according to the USGS, sauger are more phenotypically similar to walleye than yellow perch, thus making their identification more difficult. Diagnostic characteristics used to separate the two are shown in Fig. 1.

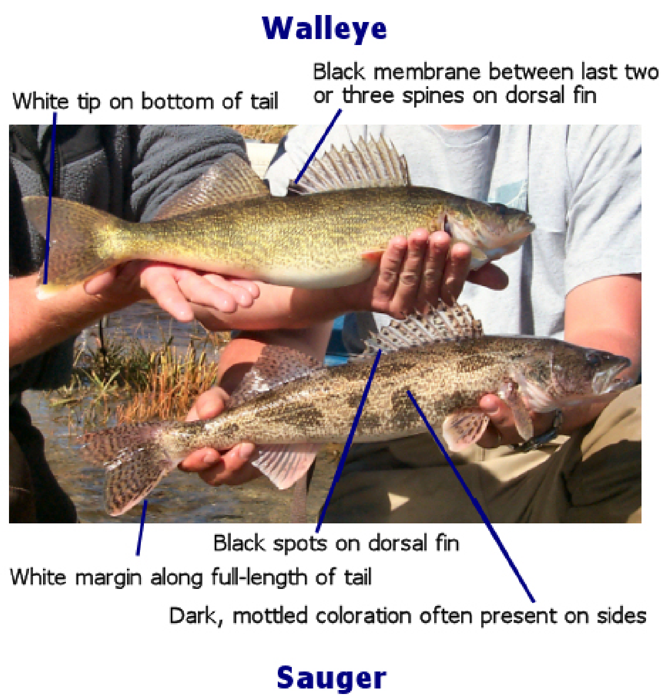

Fig. 1 Defining characteristics used to distinguish walleye from sauger (Wyoming Game and Fish Dept)

Life History and Ecology

Reproductive Strategies

Walleye spawn annually in the spring, shortly after ice-out, when water temperatures reach 4-11° C (Wolfert et al. 1997). Spawning generally occurs in water less than 3 meters deep, in areas where sediments allow for sufficient oxygen exchange for the developing embryos (Colby et al. 1979). These areas may include river mouths, sand bars, reefs, shorelines, or shallow bays. Female walleye tend to mature later, and reach a larger size at maturity than males. Presumably, this adaptation allows females to invest a larger amount of energy into gonad production than males (Henderson et al. 2003). On average, female walleye produce approximately 60,000 eggs/kg body weight (Barton and Barry 2011). Walleye broadcast spawn at night, with the female often releasing all of her eggs over the course of one, or a few nights (Ellis and Giles 1965). After spawning, neither parent exhibits any parental care for the developing embryos (Balon et al. 1977).

Life Cycle

Once fertilized, the eggs (1.3-2.1 mm in diameter) settle into crevices in the substrate, where they can develop with some protection from predators (Colby et al. 1979). The incubation period for walleye eggs is highly variable, with temperature seeming to control the number of days it takes for the embryos to hatch. In Ontario, it was concluded that eggs typically hatched 12-18 days after fertilization (Scott and Crossman 1973, Kerr et al. 2004). An experimental manipulation of temperature on developing walleye eggs showed a strong negative correlation negative between

Temp (*C*)	Egg survival[b] (%)	Abnormal fry (%)	Days to first hatch
6.0	84.0	1.0	30
8.9	66.5	3.8	23
12.0	61.5	3.3	12
15.0	15.0	1.0	8
18.1	32.0	15.0	6
20.9	0.0	18.0	5[e]

Table 1 Effects of temperature on walleye eggs and fry held at a constant temperature (adapted from Koenst and Smith Jr. 1997)

temperature and days to hatch (Koenst and Smith Jr. 1976) (Table 1).

Larval walleye are 6.0-8.6 mm long when they first emerge (Scott and Crossman 1973). Newly emerged larvae are weak swimmers and are at the mercy of the currents influencing the littoral zone (Houde and Fourney 1970). Within 1-2 weeks of hatching, larval walleye are strong enough swimmers that they can distribute themselves, instead of being transported by the currents (Colby et al. 1979). Through a series of experiments, Bulkowski and Meade et al. (1983) were able to determine that larval walleye were extremely attracted to light at this point in their development. This supported the belief that larval walleye migrated to the limnetic zone during this life stage. In the same series of experiments, Bulkowski and Meade et al. also determined that walleye older than 8 weeks were negatively phototactic, supporting the notion that walleye move to deeper water during this stage in development, where they remain for much of their lives.

Minimum size at maturity is approximately 280 mm FL in males, and slightly larger for females (Scott and Crossman 1973). However, walleye growth is highly variable, and not all fish reach this size at the same age. One factor that influences growth is temperature. A study of walleye populations in Kansas reservoirs by Quist et al. (2003), showed an inverse correlation between increasing latitude (accompanied by increasingly colder temperatures) and walleye growth rates. A study in Alabama also provided similar results (Billington and Macenia 1997).

Experts also believe that high densities of walleye can inhibit growth. A study in Big Crooked Lake, Wisconsin supported this belief by providing evidence that high-density walleye populations took longer to reach maturity than populations with lower densities (Schueller eat al. 2005). On average, male walleyes reach maturity in 2-4 years, while it takes females an average of 3-6 years (Scott and Crossman 1973). However, we do need to keep in mind that age at maturity is highly variable and dependent on local biotic and environmental conditions, as evident by populations in Northern Quebec taking up to 15 years to mature (Venturelli et al. 2010). The average longevity of walleye is 12-15 years in their northern portion of their range, and 5-7 years in the far southern boundary (Colby et al. 1979).

Feeding Habits

Age-0 walleye begin feeding before their yolk sacs are completely used up, targeting primarily planktivorous Cladocera and Copepoda in addition to a small proportion of fish (Houde 1967, Buckley et al. 1976). As the larvae grow, they become increasingly selective for large cladocerans over smaller copepods. This is likely a mechanism that allows young walleye to maximize energetic efficiency (Johnston and Mathias 1994). A recent experiment showed that fish and benthic invertebrates became increasingly important in larval walleye diets for 40-100 mm fish. The same study also determined that walleye exclusively chose fish when presented with plankton and benthic invertebrates as well (Garlowicz et al. 2006). As walleye older than 8 weeks are highly sensitive to light, it is intuitive that they are inactive and seek refuge during the day and become active during periods of low light. Strong evidence of increased foraging activity during crepuscular periods was presented by the Kelso et al. (1976) study, which used ultrasonic tracking to monitor diel movements of walleye.

In the native range of walleye, yellow perch is the most commonly consumed fish species, although their opportunistic nature leads them to prey upon a wide array of fishes, including sunfishes (Centrarchidae *spp*.), darters (Anhingidae *spp*.), gizzard shads (*Dorosoma spp.*), and minnows (*Pimephales spp.*) (Lyons 1987, Frey et al. 2003, Kolar et al. 2003).

Significant cannibalism on young walleye has even been observed (Chevalier 1979, Hansen et al. 1998). In their introduced range in the Pacific Northwest, walleye consume juvenile trout and salmon (Salmonidae *spp.*) (see section 5c.), suckers (Catostomidae *spp.*), and sculpins (Cottidae *spp.*) among other species (Poe et al. 1991, Vigg et al. 1991, Baldwin et al. 2003).

Environmental Optima and Tolerances

Although they have proven to be highly adaptable, McMahon (1984) suggests that walleye prefer "moderate-to-large lacustrine (> 100 ha) or riverine systems characterized by cool temperatures, shallow to moderate depths, extensive littoral areas, moderate turbidities, extensive areas of clean rocky substrate, and mesotrophic conditions". (McMahon et al. 1984). To achieve maximum growth, both adult adult walleye prefer temperatures between 20-24°C, with the upper lethal limit approximately 31°C (Barton and Barry 2011). Walleye are highly sensitive to levels of dissolved oxygen (DO). Both the fry and embryo stages require DO concentrations of at least 5.0 mg/L to grow and develop normally, with concentrations of less than 3.4mg/L can delay growth and ultimately lead to death. Adults also prefer DO concentrations of at least 5.0 mg/L, however they can tolerate low levels of DO better than their younger counterparts, experiencing lethal levels of DO at less than 1.0 mg/L (McMahon et al. 1984). Unlike concentrations of DO, walleye are not sensitive to pH, with all stages being able to tolerate between 6.0 and 9.0 (Colby et al. 1979).

Biotic Associations

In its native range, walleye do not experience much predation except from yellow perch on larvae, and from larger northern pike (*Esox Lucius*) (Scott and Crossman 1973). In my literature review on the subject, I could not find any significant competitors of walleye in their introduced range. Walleye are host to dozens of different parasites. In their native range one of the more common diseases is dermal sarcoma. The disease causes small warts to form on the tissue of spawning adults. Rates of mortality are unknown as is if the disease has dispersed past its native distribution with any walleye.

Geographic Distribution and Invasion History

Native Distribution

In their native range, walleye can be found from the McKenzie River in the Northwest Territories, to as far south as the Gulf Coast of Alabama (Colby and Nepszy 1981). The Appalachian and Rocky Mountains bound the eastern and western distribution of walleye, respectively (Regier et al. 1969). The heart of their range includes the states and territories surrounding the Great Lakes and the Mississippi River basin.

Non-Native Distribution

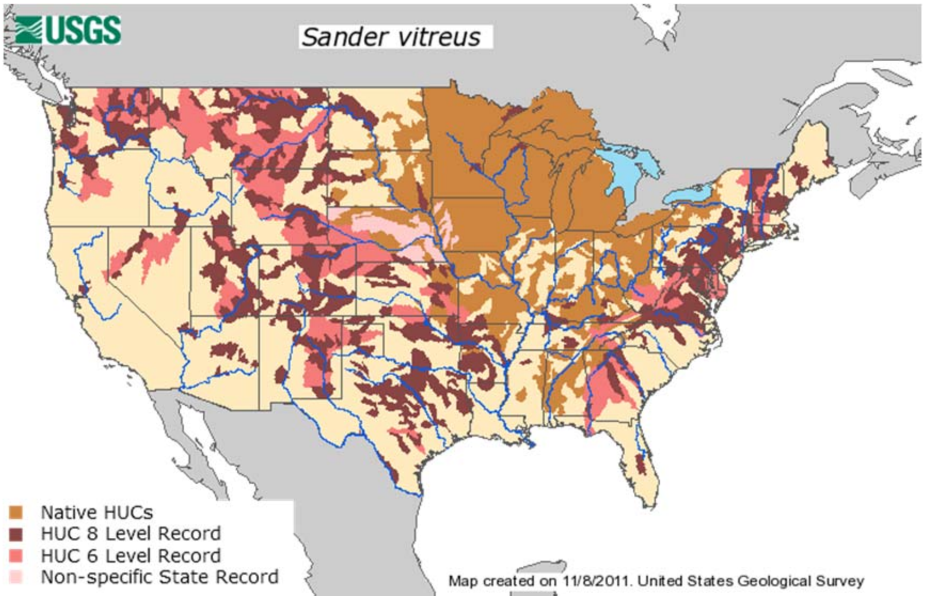

Fig. 2 Distribution of walleye in the United States. Areas with labeled with HUC 6 represent invasive populations identified at the basin level and areas labeled with HUC 8 represent invasive populations identified at the sub-basin level (USGS).

Walleye are now widely distributed throughout North America, dispersing past the previously impassable barriers of the Appalachian and Rocky Mountains (Fig. 2). Established populations of walleye now exist in 42 states throughout the nation (XXXX). In the Pacific Northwest, walleye are present throughout the Columbia River watershed. Additionally, walleye can be found in the Salmon Falls Reservoir and Bear River drainage in Southern Idaho.

Invasion History

North American Invasion

The first walleye were intentionally transplanted outside of their native range in 1874 during the "Train Car Era". During this time, the U.S. Fish Commission moved sportfishes from the East Coast to the West Coast, in order to increase angling opportunities. In June, 16 adult walleye were taken from the Missiquoi River, Vermont and translocated to the Sacramento River, California (Dill and Cordone 1997). Although the introduction failed, this was merely the beginning of nation-wide transport of walleye.

Since the original introduction attempt, walleye have been encountered throughout the U.S. Although walleye have been found in nearly all of the contiguous states, it is unknown if some of these states support established populations. A recent survey conducted by the Ontario Ministry of Natural Resources revealed that 36 states and 5 Canadian provinces stocked walleye into their waters in 2006 (Kerr 2008).

Pacific Northwest Invasion

Washington

Presently, walleye are broadly distributed throughout the Pacific Northwest (Fig. 4). The first walleye in the Pacific

Northwest were likely introduced into Lake Roosevelt in the early 1950's (Baldwin et al. 2003), likely with the intention of establishing a fishery. The introduction was not authorized and the person or group responsible for this introduction is unknown. The population in the reservoir quickly took off and walleye are currently the most abundant piscivore in the Columbia River reservoir (McLellan and Scholz 2002). In addition to expanding their population within Lake Roosevelt, walleye have dispersed throughout the Pacific Northwest since their original introduction. In the 1960's, walleye were first confirmed in Banks Lake, a nearby reservoir, which receives pumped water from Lake Roosevelt (Bennett 1979). Walleye have since dispersed downstream into the lower Columbia River and up the adjacent Snake River (Zimmerman and Parker 1995). Although walleye have become established approximately 12 reservoirs in the eastern part of the state (WDFW), they have had difficulties establishing populations in natural lakes. However, in 2005, the first documented walleye was caught in Lake Washington (Fig. 3). Subsequently, anglers and University of Washington researchers have caught more walleye from the lake (D.A. Beauchamp, UW, personal communication). Experts believe that fisherman transported these walleye from the eastern part of the state in livewells, with the hope of establishing a viable population for angling in Lake Washington (D.L. Garrett, WDFW personal communication). It is currently unknown if a self-sustaining walleye population will become established in Lake Washington.

Fig. 3 The first recorded walleye in Lake Washington. Photo: N.C. Overman

Idaho

The first introduction of walleye into Idaho occurred in 1974 when the Department of Fish and Game stocked walleye into Salmon Falls Reservoir and Mud Lake (IDFG 1982). The stocking continued through 1979 and expanded to Oneida Reservoir. Although the Mud Lake introduction failed, the Salmon Falls and Oneida Reservoir populations persisted, and have since spread throughout the Bear River Drainage in southeastern Idaho (IDFG 1982).

Oregon

The only established populations of walleye in Oregon exist in the Columbia River, with the area upstream of the John Day Dam supporting an exceptionally healthy population (Beamesderfer and Rieman 1991). These populations likely arose from individuals from

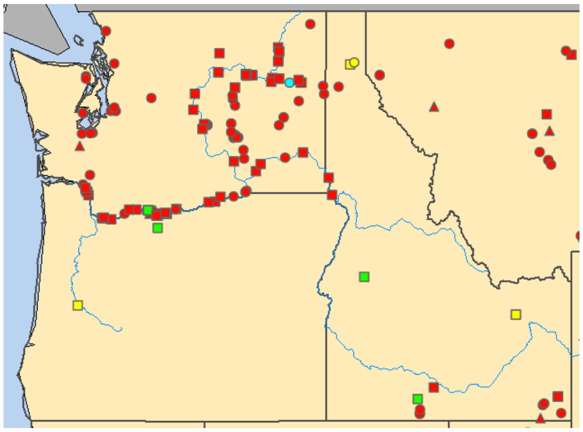

Fig. 4 Documented walleye occurrences in Washington, Oregon, and Idaho (USGS)

the original Lake Roosevelt stocking, which migrated downstream.

Invasion Process

Pathways, Vectors, and Routes of Introduction

Stocking for recreation and food accounts for the vast majority (if not all) of walleye introductions. According to the Washington Department of Fish and Wildlife (WDFW), walleye are a popular sport fish due to their “exquisite flavor and large size”. In fact, in some areas, walleye are the most desired species for eating (Schneider et al. 2007). These qualities are a major reason for the walleye’s widespread introductions. While the vast majority of introduced walleye may have been spread through intentional stocking, multiple vectors are at play in the transport of walleye.

The primary vector associated with walleye stocking is that of legal introductions. As previously mentioned in Section 4a., the U.S. Fish Commission was originally responsible for moving the first walleye (among other fishes) outside of its native range. Present day, state agencies such as the Department of Fish and Game (DFG) and the Department of Natural Resources (DNR), have taken over as the primary vectors for walleye introduction.

In a survey conducted by Bennet and McArthur (1990), 58 state and provincial agencies, spread throughout the U.S. and Canada were asked to fill out a questionnaire regarding walleye stocking practices of their respective agencies. Of the 51 that responded, 43 (86%) admitted that their agency had introduced walleye into a water body were walleye were previously absent. Additionally, 28 of those 43 agencies (66%) responded that one of these introductions resulted in an established population. Although many walleye stocking programs are intended to supplement native populations, invariably, many programs aim to spread walleye beyond of their native range. In the Pacific Northwest, Idaho is the only state that currently stocks walleye into its waters. With 869,000,000 walleye stocked in 41 jurisdictions by state and provincial agencies (Kerr 2008), it seems likely that walleye will continue to persist outside of their native range.

The other vector associated with stocking is that of illegal introductions. Illegal introductions are defined as “unauthorized, intentional release of aquatic animals to facilitate a fishery”(Johnson et al. 2009). Although the volume of illegal introductions may not be close to he magnitude of authorized introductions, illegal introductions can still yield established populations of non-native fishes. Walleye introduction in Lake Roosevelt, Washington is a great example of how "bucket biologists" can significantly aid a non-native species in their spread, as walleye are now present in the majority of the Columbia River basin.

Factors Influencing Establishment and Spread

Walleye have been successful invaders across the United States for a number of reasons. For one, they possess the most consistent attribute of an invasive species, human commensalism (J.D. Olden, personal communication). As one of North America's most popular sport fishes, it receives high propagule pressure (hundreds of millions of fingerlings stocked nationwide each year) from state agencies in order to meet angler demand, thus significantly increasing its chances of spreading. Other attributes of walleye that allows it to successfully invade include its broad diet (Section 2c.), rapid growth in warm temperatures (Section 2b.), and its wide environmental tolerance (as exhibited by a distribution that spans 40° of latitude).

In addition to possessing attributes that made it a successful invader, walleye were able successfully invade the Pacific Northwest due in part to a lack of resistance from the biotic community of the host environment. The only large piscivores in the Pacific Northwest that could possible pose a threat to introduced walleye, either through competition or direct predation, are native northern pikeminnow (*Ptychocheilus oregonensis*) and non-native smallmouth bass (*Micropterus dolomieu*). However, a previous study of competition between walleye and smallmouth bass in their sympatric native range showed that smallmouth bass did not prey on juvenile walleye and the diet overlap between the two was not significant. On top of this, one walleye even had a smallmouth bass in its stomach (Frey et al. 2003). Northern pikeminnow has proven to be an equally weak competitor to walleye. A study on the John Day Reservoir showed that walleye tended to consume sculpins and suckers, while northern pikeminnow preferred salmonids and crustaceans (Crustacea *spp.*). In conjuction with this, there has been no evidence of northern pikeminnow predation on walleye. A lack of competition from both native and non-native fishes of the Pacifc Northwest has allowed walleye to thrive.

Potential Ecological and Economic Impacts in the Pacific Northwest

Both the ecological and economic impacts of walleye in the Pacific Northwest revolve around salmonids. Studies in the Columbia River have shown that walleye are significant preadtors of out-migrating Pacific salmon (*Oncorhynchus spp.*) and steelhead (*Oncorhynchus spp.*) smolts, contributing to over 20% of walleye diet in some instances (Poe et al. 1991, Vigg et al. 1991). A study by Rieman et al. (1991) took it a step further by combining data on walleye abundance and predation rates on smolts to estimate the total salmonid loss due to walleye predation in the John Day Reservoir. They estimated that walleye contribute to the annual loss of 351,000 out-migrating smolts, with 429,000 being the high estimate. Not only do walleye pose a serious threat to already declining populations of salmon, but they also have the potential to damage the economy that Pacific Salmon create. In 2005, the Columbia River basin salmon fishery was estimated to be worth $142 million (IAEB) to local Pacific Northwest communities. Additionally, the IAEB estimated that the revenue brought in by the fishery could support 3,3633 jobs. The loss of the revenue and jobs created by the Columbia River basin salmon fishery would be a huge blow to the economies of Washington, Oregon, and Idaho. Although it is not likely that walleye can single-handedly wipe out the entire Columbia River salmon run, it is plausible that they could accomplish this in conjunction with other human mediated changes to the basin such as impoundment, pollution, and climate change.

Management Strategies and Control Methods

As I may have alluded to in previous sections, non-native walleye have not been treated as a non-native fish. Traditionally, management strategies of walleye have focused on expanding their range, rather than trying to eradicate them as a nuisance species (Goeman 2002). The overall feeling of the general public toward walleye becomes evident when you try to conduct a literature search on "invasive walleye". Placing the term "invasive" in front of walleye in a scientific article would likely ruffle the feathers of enough readers to make it not worth publishing. Instead, one must use gentler adjectives such as "non-native" or "introduced" and even then, articles are hard to come across. It seems as though walleye are so widely distributed, and have been for a period of time, that we seem to have forgotten that they are indeed highly invasive in some areas and have the potential to cause major ecological and economic impacts. I was unable to find any methods being used to control walleye outside of their native range, although many groups and agencies stated that they were monitoring non-native walleye.

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Other Resources

Idaho Department of Fish and Game Historical Stocking Records
http://fishandgame.idaho.gov/public/fish/stocking/

USGS Non-Indigenous Aquatic Species
http://nas.er.usgs.gov/

Washington Department of Fish and Wildlife
http://wdfw.wa.gov/

Expert Contact Information

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Danny is a fisheries biologist who specializes in warmwater fishes. He is also assisting with the Lake Washington walleye project.

Current Research and Management efforts

As an undergraduate Dave Beauchamp's lab here at the University of Washington, I am working with Dave to further understand the potential ecological impacts that recently introduced walleye may have on Lake Washington. Of particular concern is the potential impact on salmonid smolts through walleye predation. Since May 2010, we have caught 4 walleye in the lake (one of which was generously donated by Julian Olden's lab) by gillnetting, in addition to the first recorded walleye in Lake Washington, which was captured in 2005. Only 2 out of 5 fish and prey in their stomachs upon dissection, with one having consumed a few peamouth (M*ylocheilus caurinus*), and one having consumed longfin smelt (*Spirinchus thaleichthys).* We recently said stable isotope samples in for analysis in order to reveal a larger snapshot of the feeding habits of these fish. In the future we plan on tracing the origins of these invaders through otolith microchemistry, in addition to applying a bioenergetics model to determine the overall consumptive demand of walleye on salmonid smolts in the lake.