Effects of the introduction of lake trout (Salvelinus namaycush) on the osprey (Pandion haliaetus) popoulation in Yellowstone National Park.

Effekter fra introduksjon av canadarøye (Salvelinus namaycush) på bestanden av fiskeørn (Pandion haliaetus) i Yellowstone Nasjonalpark.

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Master Thesis 30 credits 2010

Effects of the Introduced Lake Trout (*Salvelinus namaycush*) on the Osprey (*Pandion haliaetus*) Population in Yellowstone National Park.

A master thesis in Nature Resource Management

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Ås - 2010

Preface

My motivation for studying the Yellowstone osprey population and its response to the change in the aquatic ecosystem was to do a study on a topic that is of global concern today. Management issues regarding introduction of alien species is just as relevant in Norwegian ecosystems as it is in Yellowstone. The opportunity to spend a summer in the fascinating nature of Yellowstone was of course another motivating factor. The fieldwork in Yellowstone National Park did also give me an insight in a management regime somewhat different than in Norway. During the work with this thesis I have learned a lot about scientific work and how to write a scientific paper.

I would like to thanks my supervisor at the Department of Ecology and Natural Resource Management (INA), Norwegian University of Life Science (UMB), Professor Jon Swenson. Without his knowledge and contacts in Yellowstone National Park, this project would not have been possible, and without his encouragement and help, the work with this thesis would have been a hard and frustrating process. I also owe thanks to the scientists; Dr. Douglas W. Smith and Lisa Baril, park rangers; Kyle McDowell and Robert Elliot, and all the other people in Yellowstone who helped me out during my fieldwork. Last but not least I thank my family for their support and for holding on to the belief that I could find my way on the long and, sometimes, winding academic path.

Ås, 10 December 2010

Anders Søyland

Photo page one: Lake Trout caught in Southeast Arm, Yellowstone Lake, July 2010.

Abstract

In recent years the number and reproduction of ospreys (*Pandion haliaetus*) nesting on Yellowstone Lake in Yellowstone National Park (YNP), USA, has been declining. The main hypothesis is that the decline in nesting ospreys is due to the introduction of the lake trout (*Salvelinus namaycush*), which is believed to have reduced the cutthroat trout *(Oncorhynchus clarki bouvieri)* population in Yellowstone Lake substantially. The lake trout inhabit deeper water range than the cutthroat and is therefore not within reach of the ospreys. During the summer of 2010 I monitored ospreys on Yellowstone Lake to study their foraging habits and reproductive outcome. I found that the foraging behavior has changed substantially for the ospreys since the introduction of lake trout. Despite more than 60 hours of monitoring, I did not observe any ospreys foraging or attempting to forage at Yellowstone Lake. This is in contrast to the situation before the decline in the cutthroat trout population, when ospreys regularly were seen foraging at the lake. I also studied the change in numbers of nesting ospreys and their reproductive parameters in YNP, based on monitoring statistics from 1987 to 2010. The data showed a statistically significant change in distribution of both active and successful nests, on and away from Yellowstone Lake, in the period 1987-2001 vs. 2006-2010. Yellowstone Lake used to have a majority of the active nests in the park in 1987-2001, but in 2006 and 2010 there have been just a few active nests on the lake. The reproductive success from the nests on the lake also has been low in the last years. By studying catch statistics for the cutthroat trout in Yellowstone Lake, I found a significant positive correlation between the cutthroat trout population and both number of nesting ospreys and reproductive outcome. The outcome from my study supports the hypothesis that the ospreys nesting on Yellowstone Lake have been affected in a negative way by the change in the fish community. The declining cutthroat population probably has affected the foraging success of the ospreys and in turn led to reproduction failure due to lack of available fish to prey upon.

Sammendrag

De siste årene har det vært en nedgang i antall og reproduksjonen hos fiskeørn (*Pandion haliaetus*) som hekker ved Yellowstone Lake i Yellowstone Nasjonalpark, USA. Hovedhypotesen er at nedgangen i hekkebestanden skyldes introduksjon av canadarøye (*Salvelinus namaycush),* som man tror har forårsaket en kraftig bestandsnedgang av cutthroat trout (*Oncorhynchus clarki bouvieri*) i Yellowstone Lake. Canadarøya står dypere i vannmassene enn cutthroat trout, og er derfor utenfor fangstrekkevidde for fiskeørnen. I løpet av sommeren 2010 observerte jeg fiskeørnbestanden ved Yellowstone Lake, med hensikt å studere næringssøk og reproduksjon. Jeg fant ut at fangstadferden til fiskeørnene har forandret seg markant. På tross av mer enn 60 timer med observering, så jeg ikke en eneste fiskeørn som fanget fisk eller forsøkte å fange fisk på Yellowstone Lake. Dette står i sterk kontrast til situasjonen før nedgangen i bestanden av cutthroat trout, da det reglemessig ble observert fiskeørner som fanget fisk i innsjøen. Jeg studerte også forandringen i bestandsantall og reproduksjon hos hekkende par fiskeørn i Yellowstone Nasjonalpark, basert på overvåkningsdata fra 1987 til 2010. Dataene viste en statistisk signifikant forandring i fordelingen av både aktive og suksessfulle reir, på og utenfor Yellowstone Lake, i perioden 1987-2001 kontra perioden 2006-2010. I perioden 1987-2001 var majoriteten av aktive fiskeørnreir i Yellowstone lokalisert ved Yellowstone Lake, mens i 2006 og 2010 har det bare vært et par reir ved innsjøen. Reproduksjonen fra reirene ved Yellowstone Lake har også vært lav de siste årene. Ved å studere fangststatistikk for cutthroat trout I Yellowstone Lake, fant jeg en signifikant positiv korrelasjon mellom bestanden av cutthroat trout og både antall hekkende fiskeørn og reproduksjonssuksess. Resultatet fra mitt studie bygger opp under hypotesen om at hekkebestanden av fiskeørn ved Yellowstone Lake har blitt negativt påvirket av forandringen i fiskesamfunnet. En nedgang i bestanden av cutthroat trout har trolig påvirket fangstsuksessen til fiskeørnene og dermed ført til reproduksjonssvikt på grunn av dårlig næringstilgang.

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Introduction

Invasive alien species that take hold in foreign habitats and become aggressive to the indigenous species, are recognized as one of the greatest threats to the biodiversity of the planet (Mooney & Hoobs 2000). Invasive species are also considered to have extensive negative impacts on human economic interests. In the US alone invasive species are estimated to have an economic cost of $137 billion per year (*Global Invasive Species Programme* 2010). In freshwater systems nonindigenous species can cause severe impacts on the ecosystem. With increased globalization, anthropogenic movement of alien species has begun a homogenization of the world's freshwater biota (Mooney & Hoobs 2000). Establishment of alien freshwater species not only impacts the aquatic biota, but can also affect birds and terrestrial animals utilizing the aquatic resources (Mooney & Hoobs 2000; Varley & Schullery 1995). In Yellowstone Lake this is the case with the recent introduction of lake trout (*Salvelinus namaycush*). Through predation, the lake trout has suppressed the native cutthroat trout (*Oncorhynchus clarki bouvieri*) population. This shift in the freshwater ecosystem is believed to affect several terrestrial and avian predators foraging on the cutthroat (Varley & Schullery 1995).

Yellowstone National Park (YNP) includes most of the current range of the Yellowstone subspecies of cutthroat trout (Gresswell 1995; Varley & Gresswell 1988). Yellowstone Lake, together with the Yellowstone River, contains the largest population of inland cutthroat trout in the world (Young 2010). Because of its important role as prey for fish-eating scavengers and predators, the cutthroat trout is a key species of the Yellowstone ecosystem. The cutthroat trout provides an important link to the terrestrial ecosystem, and a wide range of birds and mammals are dependent on it as a source of protein (Ruzycki et al. 2003; Varley & Schullery 1995). In the Yellowstone ecosystem 42 species of birds and mammals use cutthroat trout as a food resource (Varley & Schullery 1995). Crait and Ben-David (2009) found that cutthroat trout was the most common prey species of river otters (*Lontra canadensis*) in Yellowstone, and Koel et al. (2005) suggested that the cutthroat population is an important energy source for grizzly bears (*Ursus arctos horribills*). The white pelican (*Pelecanus erythrorhynchos*), bald eagles (*Haliaeetus leucocephalus*), ospreys (*Pandion haliaetus*) are some of avian predators in YNP known to prey upon the cutthroat (Gresswell 1995, Swenson et al. 1986, Swenson 1978). Swenson (1986) found that cutthroat trout comprised 12.5% of the total prey species utilized Bald Eagles. He also found that cutthroat trout comprised 93% of the diet of ospreys on Yellowstone Lake (Swenson 1978).

In this study I examine the changes in the Yellowstone osprey population in relation to the status of the cutthroat trout population. Reports indicate that the ospreys nesting on Yellowstone Lake have experienced a downward trend the last ten years, this is in contrast to the ospreys nesting elsewhere in the park (Baril et al. 2010; McEneaney 2007). Yellowstone Lake used to have the highest density of nesting ospreys (*Pandion haliaetus*) in YNP, but the last years the number of active nests has declined to just a few nests (Baril et al. 2010; Baril 2009; McEneaney 2000). Based on annual reports and historical data, I examined the relationship between the osprey population and the cutthroat population. I also observed ospreys on Yellowstone Lake to document their foraging behavior and reproduction success. My hypothesis is that the declining cutthroat population has affected the reproduction in the osprey population in a negative way, due to a lack of suitable fish for foraging. Low productivity should thus have led to the decrease in the nesting population of ospreys on Yellowstone Lake.

Study Species

Osprey

The osprey is the only species in the genus *Pandion.* It has a worldwide distribution and breeds in all continents except from Antarctica. The body size of the osprey ranges from 55 to 58 cm and it has a wing span from 145 to 170 cm. The female is typically 5-10 % larger than the male (Cramp 1980). It is a specialized fish eater that breeds both in coastal and inland waters. The osprey catches its prey in its talons after shallow dives not deeper than 1 m. The dives are commonly made from 20-30 m above the surface *(Cramp 1980)*. Swenson (1978) found that immature cutthroat trout ranging from 25 to 35 cm in size were preferred prey by the Yellowstone Lake ospreys. In a study in Idaho Van Daele & Van Daele (1982) found that fish between 11 and 30 cm comprised the largest proportion of the osprey's diet. Ospreys nest in tree-tops or snags or on artificial sites such as power poles and artificial nesting platforms (Van Daele & Van Daele 1982).

The number of nesting pairs of ospreys in YNP has fluctuated during the last three decades, from a maximum of 100 in 1994 to a minimum of 24 in 2008 (Baril 2009; McEneaney 2000). The reproduction of the osprey population declined in the period 1987-2003, but increased since 2003 (Baril et al. 2010). Baril (2009) proposed that the declining cutthroat population plays a significant role in determining the reproductive outcome of the ospreys on Yellowstone Lake. In a study from Cheasapeake Bay, McLean and Byrd (1991) found that limiting food caused increased sibling aggression, brood reduction, and decreased growth of the young. Weather and tree nest stability are other factors that can influencing the reproduction. This was demonstrated in YNP in 2004 when strong winds destroyed many nest trees and caused high reproduction failure (McEneaney 2005). Distance from human disturbance can also affect the productivity. Swenson (1979) found that nest success of ospreys in YNP was significant higher for nests located more than one km away from a campsite. Van Daele & Van Daele (1982) reported that ospreys nesting 1500 m from human disturbances where the most productive.

From annual reports made by the National Park Service (NPS), it seems that the number of fledged young ospreys experienced a massive drop from around 2000 until 2003 (Baril et al. 2010; McEneaney 2005). In 2009 The National Park Service monitored 27 osprey nests within YNP. Of those 48% successfully fledged a total of 28 young. On Yellowstone Lake only four pairs nested in 2009 and none of those succeeded in fledging (Baril et al. 2010). In contrast, 59 nesting pairs of osprey, fledging 26 young, were reported on Yellowstone Lake in 2001 (McEneaney 2002).

A 23-year average of the productivity of the osprey population in YNP is 0.78 young per active nest (Baril et al. 2010). This is lower than the level calculated by Henny and Wight (1969) to be the critical productivity level to maintain a stable population. They found the critical productivity level to be between 0.95 and 1.30 young per nest.

Yellowstone cutthroat trout

The cutthroat trout in Yellowstone Lake and its tributaries has remained genetically pure, due to isolation by the Lower and Upper Falls of Yellowstone River (Koel et al. 2005). From May to July mature cutthroat trout used to ascend about half of 126 tributaries in Yellowstone Lake to spawn (Varley & Gresswell 1988). However, recent studies have revealed a decline in the number of cutthroat trout spawning in Yellowstone Lake tributaries (Haroldson et al. 2005; Koel 2010). The spawning cutthroat trout remain in the streams from one to three weeks (Bal and Cope 1961, cited by Varley & Gresswell 1988). Fry emerges about 30 days after egg deposition. Most of the fry migrate to the lake within two months after deposition, but some remain in the natal stream for one or two years (Benson 1961, cited by Varley & Gresswell 1988). Larger Yellowstone cutthroat are resident in the littoral zone throughout the year (Varley & Gresswell 1988).

Human activities have reduced the range of the Yellowstone cutthroat trout to 15% of the historical distribution (Varley & Schullery 1995), and the remaining population faces several threats. In streams throughout YNP the genetic purity of the Yellowstone cutthroat trout is threatened by mixing with other cutthroat subspecies and other trout species, such as the nonnative rainbow trout (*Oncorhynchus mykiss*) (Koel et al. 2005). In 1998 *Myxobolus cerebralis* was discovered on the cutthroat trout in Yellowstone Lake. This exotic parasite is the cause of whirling disease, responsible for severe declines in wild trout populations in the U.S. (Koel et al. 2006). The cutthroat trout is also affected by aridity changes, caused by multiannual drought periods in the western U.S (Cook et al.

2004). Maybe the most serious threat for the Yellowstone cutthroat trout however, is the introduction of the invasive lake trout (Koel et al. 2005).

Lake trout

The lake trout is a benthopelagic, nonmigratory species that lives in depths from 18 to 53 m (Froese & Pauly 2010). It can reach lengths up to 150 cm, but the most common length is about 50 cm. The lake trout is widely distributed in North America, ranging from northern Canada and Alaska south to New England in the USA (Froese & Pauly 2010). In Yellowstone Lake the first discovery of lake trout was found in 1994, but it was probably introduced to the lake in the 1980s (Young 2010). Since its introduction, the lake trout has spread throughout the lake (Shaw et al. 2004) and it now occupies the entire lake (Doepke 2010 pers. com).

The lake trout is considered to pose the greatest threat to the cutthroat trout and the lake ecosystem (Ruzycki et al. 2003; Young 2010). Young lake trout eat the same macroinvertebrate food as the cutthroat trout (Varley & Schullery 1995), and it has been documented that the lake trout is a considerable predator on cutthroat trout (Koel 2010; Ruzycki et al. 2003). Ruzycki et al. (2003) found that fish, primary cutthroat trout, comprised 60% of the diet of 3-4-year-old lake trout, whereas the proportion was 95% for lake trout older than 9 years. The same study estimated that each lake trout above five years annually consumed more than 40 cutthroat trout. This consumption by lake trout constituted for 10% of the annual production of the cutthroat trout population in 1996, but by 1999 the consumption was reduced to 7% due to the National Park Service control program (Ruzycki et al. 2003). A demographic model made by Stapp and Hayward (2002) predicted a decline in the cutthroat trout population of 60% or more within 100 years without control action.

The fact that the lake trout does not spawn in streams and inhabits relatively deep water, makes it unavailable to terrestrial predators such as the osprey, and it will therefore not be an ecological substitute for the cutthroat trout in Yellowstone Lake (Koel et al. 2005; Varley & Gresswell 1988).

Study area

Yellowstone National Park

Yellowstone National Park was established in 1872, as the world's first national park. It is also a designated World Heritage site and a Biosphere Reserve site. Yellowstone National Park is a part of the Greater Yellowstone Ecosystem. Covering approximately 45,000 km^2, this is one of the world's largest intact temperate ecosystems. The National Park covers 8,987 km^2, of that 96% is located in Wyoming, with Montana and Idaho comprising respectively 3% and 1% (Young 2010) (Fig 1). About 80% of the park is covered by forest, predominately lodgepole pine (*Pinus contorta*). The lodgepole forest has a sparse understory dominated by elk sedge (*Carex geyeri*) or grouse whortleberry (*Vaccinium scoparium*) (Kokaly et al. 1998; Young 2010).

The Yellowstone plateau is situated in a tectonic active area, where geological forces, such as volcanic eruptions, earthquakes and hydrothermal features, have created the physical landscape (Young 2010). The Yellowstone Caldera was formed by a volcanic eruption 640,000 years ago, and covers 85 X 45 km across YNP (*Yellowstone Volcano Observatory* 2010), including the northern part of Yellowstone Lake. The rhyolitic magma that erupted during those volcanic events has formed the nutrient-poor soil in the Yellowstone caldera (Young 2010).

Yellowstone Lake

Yellowstone Lake covers an area of 212 km^2 and has a shoreline of 227 km. At an elevation of 2357 m above sea level it is the largest high-elevation lake (> 2100 m) in North America (*National Park Service* 2010). The lake freezes in late December or early January and remains frozen until May/June. In July it forms a thermocline at a depth of 10-20 m that persists until mid September (Varley & Schullery 1995). Recent explorations of the lake have revealed depths of 118 m and a bottom consisting of geysers, hot springs and deep canyons (*National Park Service* 2010). The average depth of the lake is 48 m (Varley & Schullery 1995). It is an oligotrophic cold-water lake with surface temperatures rarely exceeding 18 ^{o}C (Benson 1961, cited by Varley & Gresswell 1988). The sparse phytoplankton community is dominated by diatoms, and the zooplankton is dominated by three species; *Diaptomus shoshone, Daphnia schøedleri* and *Conochilus unicornis* (Varley & Gresswell 1988; Varley & Schullery 1995).

The Yellowstone cutthroat trout is one of only two indigenous fish species in Yellowstone Lake, the other is the longnose dace (*Rhinichthys cataractae*) (Simon 1962, cited by Ruzycki et al. 2003). Introduced fish species include; longnose sucker (*Catostomus catostomus*), redside shiner

(*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and lake trout (Gresswell et al. 1994, sited by Ruzycki et al. 2003). According to Benson (1961, cited by Varley & Gresswell 1988) the longnose sucker was introduced to the lake in 1923 or 1924 and the redside shiner was first discovered in 1957. The lake chub was first reported in Indian Pond, near Yellowstone Lake, in 1967, but was not discovered in Yellowstone Lake until several years later (Cope 1958, cited by Varley & Gresswell 1988). Longnose suckers, redside shiners, and the lake chubs have had little negative impact on the cutthroat trout, because they apparently filled empty niches in the lake (Varley & Gresswell 1988).

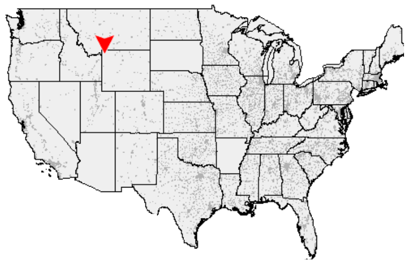

Fig. 1: Map of Yellowstone National Park. The location of the park U.S is marked with a red arrow.

Methods

Field Observations

In the summer of 2010 I spent six weeks in YNP to make visual observations of ospreys foraging on Yellowstone Lake. The field work was conducted from the start of June to mid July. I focused on Yellowstone Lake, as this area was expected to have experienced the most severe change in the osprey population. Because of logistical problems and closure of areas due to bear management, most of the time I was only able to do observations on the western side of Yellowstone Lake. Each period of monitoring lasted from one to three hours, and was conducted at different times of the day.

During the three first weeks most of the monitoring was done from observation points located near the road on the west shore of the lake. I chose observation points to give a good view of the shoreline, and to cover most of the lake from Fishing Bridge in north to Grant Village in south. I also spent time monitoring two osprey nests near the West Thumb Geyser Basin to determine if they were occupied and if the ospreys were foraging on Yellowstone Lake or elsewhere. In the last weeks of the field period, I also joined park rangers and fishery biologists out on the lake making observations from boat. I spent two days on the lake with park rangers, patrolling the lake from Bridge Bay and Grant Village, and one day with the lake trout removal crew, gillnetting along the west shore and in West Thumb. Two days where also spent in the Southeast arm. In addition to the monitoring I did, I handed out observation sheets to rangers and fishermen who spent three to five days on the lake every week.

I conducted monitoring from the shore or a boat with binoculars (Nikon Monarch 10X42 6^{o}) and a spotting scope (Nikon Fieldscope ED 13X to 75X) mounted on a tripod. If an osprey was observed, I noted the approximate point of observation and direction of flight.

Analysis of historical nesting sites data.

The National Park Service has monitored the osprey population in YNP by since the 1980s. In this monitoring program the annual numbers of active nesting pairs has been counted and reproduction rate has been recorded. The NPS provided me with data on nesting distribution and reproduction from 1987, 1991, 1996, 2001, 2006 and 2010. In the tables I also included data from Swenson's fieldwork from 1972 to 1974 (Swenson 1975). To test differences in nest distribution, chi-square tests were run in the statistical analyzing tools Minitab and SigmaStat (χ^2 with Yates correction, based on 2x2 contiguity tables).

Correlations between number of active pairs of nesting ospreys and the cutthroat trout population and between fledged young and the cutthroat trout population were analyzed by use of count data of active osprey nests in YNP, and catch statistics of cutthroat trout. Average In-lake catch of cutthroat trout per net was used as a measure of the cutthroat trout population, rather than counts of spawning cutthroat, because Swenson (1978) found that the ospreys on Yellowstone Lake were foraging primarily on immature trout.

To determine the relationship between the cutthroat population and nesting pairs of ospreys and number of young fledged, I ran Pearson correlation tests in MiniTab, using data found in annual reports made by the NPS. I chose 1994 as a starting year for the analysis, because this was also the first year lake trout were reported in Yellowstone Lake. I added time lag to evaluate the time it might take before a decline in the cutthroat trout population affects the osprey population. Several years of time lag were added to find the best fit. I ran tests with more years of time lag added until the available data was considered too low or an obvious wrong result occurred (a negative correlation).

Population terminology in this thesis follows the terminology of the Yellowstone annual Bird Reports (Baril et al. 2010; Baril 2009; McEneaney 2000; 2003; 2005; 2007). Active nests are defined as nests where ospreys have been seen incubating on the nests during aerial surveys. Successful nests are defined as nests with successful fledging of young.

Results

Field observations

From 4 June to 11 July 2010 I spent a total of 65 hours monitoring on Yellowstone Lake. I observed ospreys only occasionally and never observed them foraging or attempting to forage on the lake. The few observations I made of ospreys by the lake were done near Bridge Bay (three observations) and by the nests in West Thumb. In most cases I observed the ospreys only for a brief period before they flew out of sight; they were never in sight for more than a few minutes. In the occasions where I observed ospreys at Bridge Bay, the birds hovered over the bay for some time before disappearing out of sight. Just a few observations were made of ospreys at the lake by other persons than me. One observation was made near Fishing Bridge and another observation was reported near Mary Bay in the north end of the lake. Fishery biologists and rangers, who patrolled the lake several times a week during the summer seasons, said that ospreys have been a rare sight on the lake during the last few years (pers. com.: Doepke 2010; Elliot 2010; McDowle 2010). Doepke told me that he had never seen an osprey foraging on the lake in the seven years he had been working as a fishery biologist on the lake.

In the period 17 June to 7 July I spent 13 hours monitoring the two nests in West Thumb. In the northern nest I observed ospreys flying to and from the nest. In every occasion except from one, the ospreys flew away from the lake, disappearing out of sight before a more precise direction of flight could be determined. In the one occasion, where the osprey was flying toward the lake, it crossed the bay without any attempt at foraging, disappearing out of sight to the south. I also observed activity at the southern nest in West Thumb, but the location of this nest made it more difficult to monitor and ospreys were never observed flying to or from this nest.

On a boat patrol to Southeast Arm on 26 June, I observed ospreys hovering over the arm, but I was not able to locate the nest. On a field trip to the arm in July we found the nest, but no birds were observed in or near the nest. During aerial surveys conducted by the National Park Service, a total of three active nests were observed in the southeast parts of the lake (Fig. 2).

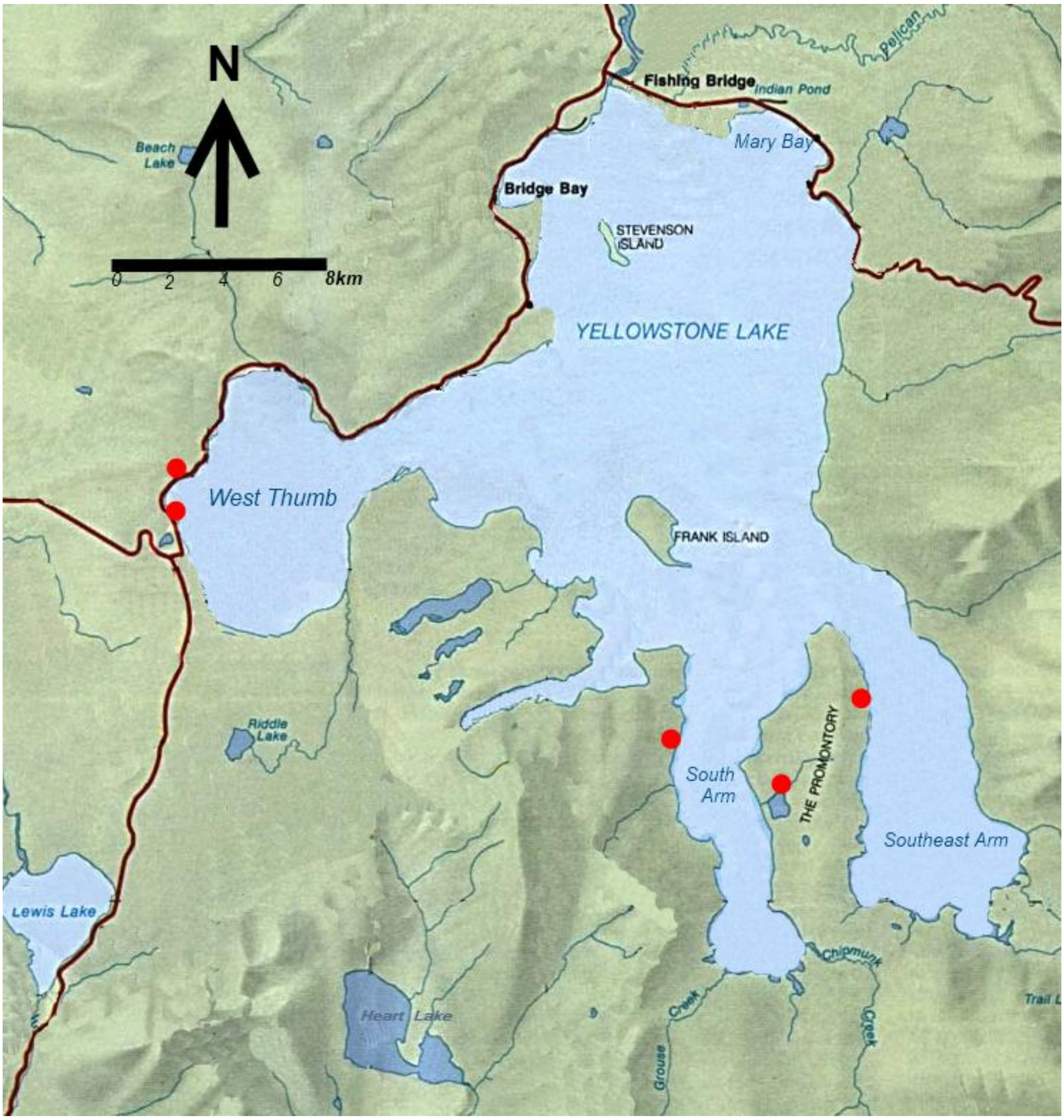

Fig. 2: Map of Yellowstone Lake and surrounding waters. Active osprey nests in 2010 are marked with red dots.

Historical monitoring data

Active nests in YNP

In 2010 a total of 30 active osprey nests were counted in YNP. Of those, 25 were located away from Yellowstone Lake and only 5 active nests were observed on Yellowstone Lake (Fig. 3). This is in contrast to the situation in 1972-1974, 1987, 1991, 1996 and 2001, when most of the nests in Yellowstone were found on Yellowstone Lake. In the period 1987 to 2010 the distribution between nest on and away from Yellowstone Lake changed significantly (χ^2= 37.130; df= 5; p<0.005). An chi-square test run separately on the years from 1987 to 2001 showed no statistically significant differences (χ^2= 0.900; df= 3; p=0.825). A chi-square test with Yates correction was run to test the change in nest distribution on and away from the lake in the period 1987-2001 vs. 2006-2010. This test showed a significant change in the distribution pattern between the two periods (χ^2= 34.3; df= 1; p<0.005). From a maximum of 60 observed nests on the lake in 2001, the number had dropped to only 10 in 2006. Also this change was statistically significant (χ^2 with Yates correction=15.2, df=1 P<0.0001).

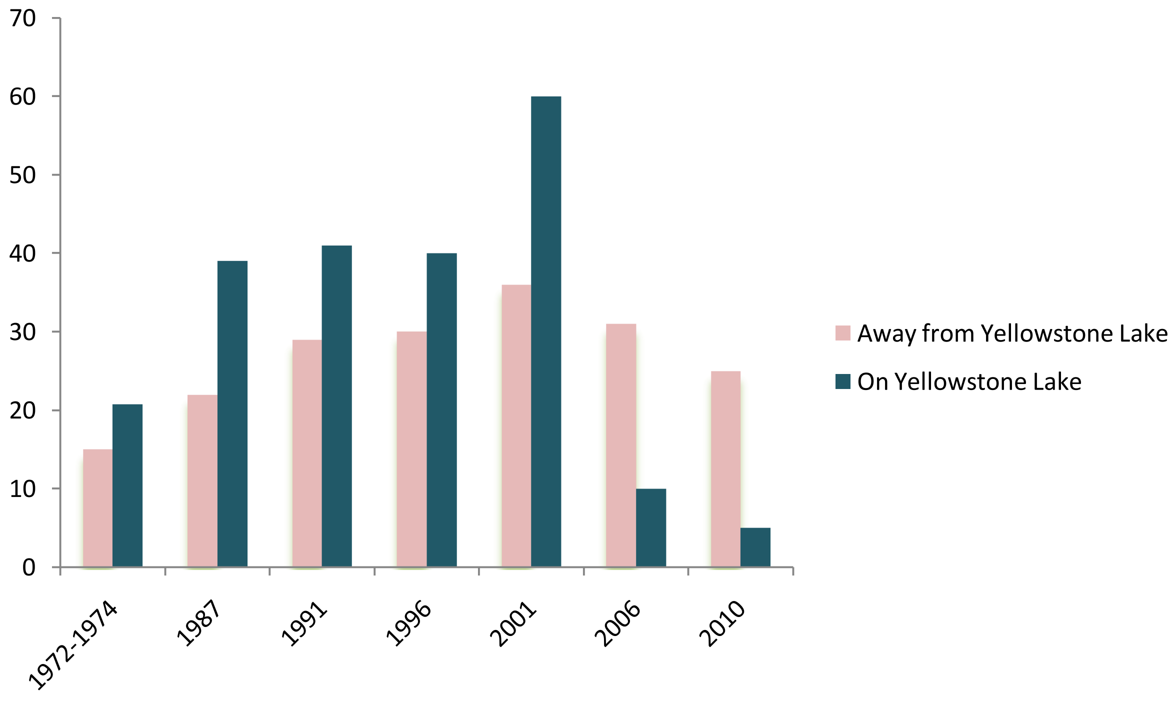

Fig. 3: Active osprey nests on and away from Yellowstone Lake 1927-2010. The counts for 1972-74 are average numbers for this period (Swenson 1975).

Successful nests in YNP

Of the 30 active nests in YNP in 2010, 16 nests had successful reproduction. In the monitored years the number of successful nests outside Yellowstone Lake has fluctuated from a minimum of 11 in 2006 to a maximum of 17 in 2001 (1972-1974 not included). On the lake the number of successful nests has fluctuated from a maximum of 25 in 1991 to no successful nests in 2010. A significant change in the distribution of successful nests on and away from the lake was found between the periods 1987-2001 and 2001-2010 (χ^2 with Yates correction=18, df = 1, P<0.0001, Fig. 4).

Even though the total number of successful nests has been lower in the recent years, the percent of the active nests that had a successful reproduction was almost as high in 2010 as in 1991 (Fig. 5). In 2010 the nests away from Yellowstone Lake had a success rate of 64%. Including the five unsuccessful nests on Yellowstone Lake, the overall success rate for YNP was 53% in 2010.

Young fledged in YNP

In 2010, 36 young fledged successfully from osprey nests in YNP. In contrast 71, young were fledged in 1987. No young were fledged from the nests on Yellowstone Lake in 2010, but nesting ospreys outside the lake fledged more young in 2010 than in any of the other monitoring year (Fig. 6). The change in the distribution of young fledged between nests on and away from Yellowstone Lake was statistically significant in the period 1987 to 2010 (χ^2 = 46.677; df = 5; P < 0.000).

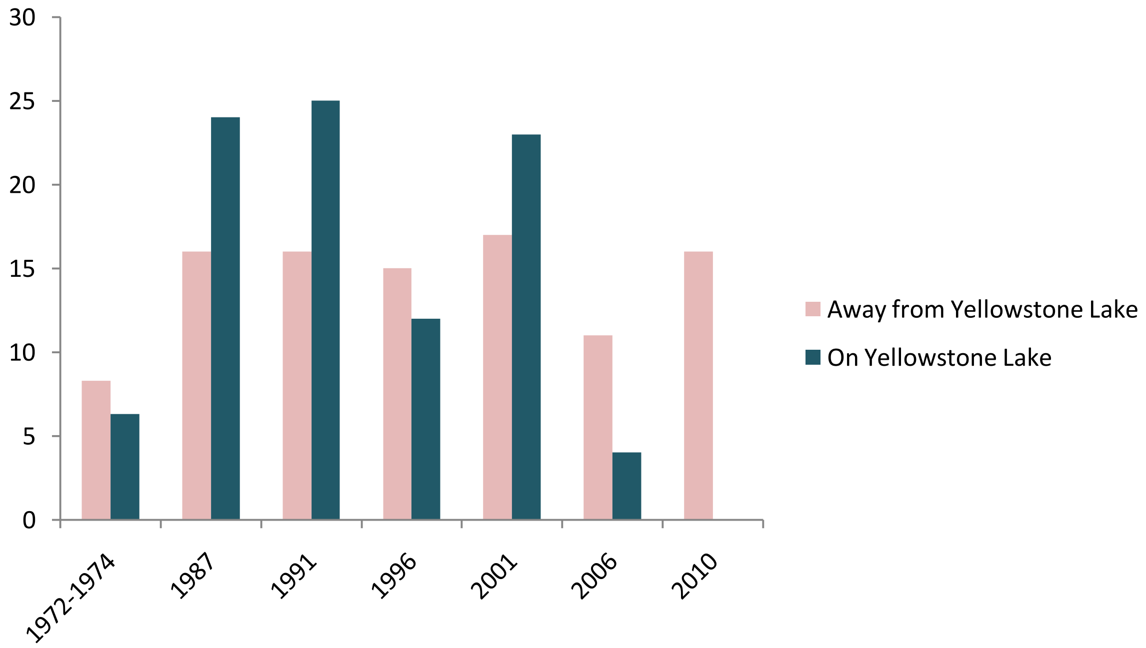

Fig. 4: Number of successful osprey nests on and away from Yellowstone Lake during 1972-2010. The counts for 1972-74 are average numbers for this period (Swenson 1975).

Fig 5: Percent of osprey nests with successful reproduction, on and away from Yellowstone Lake and totally, during 1972-2010. The counts for 1972-74 are average numbers for this period (Swenson 1975).

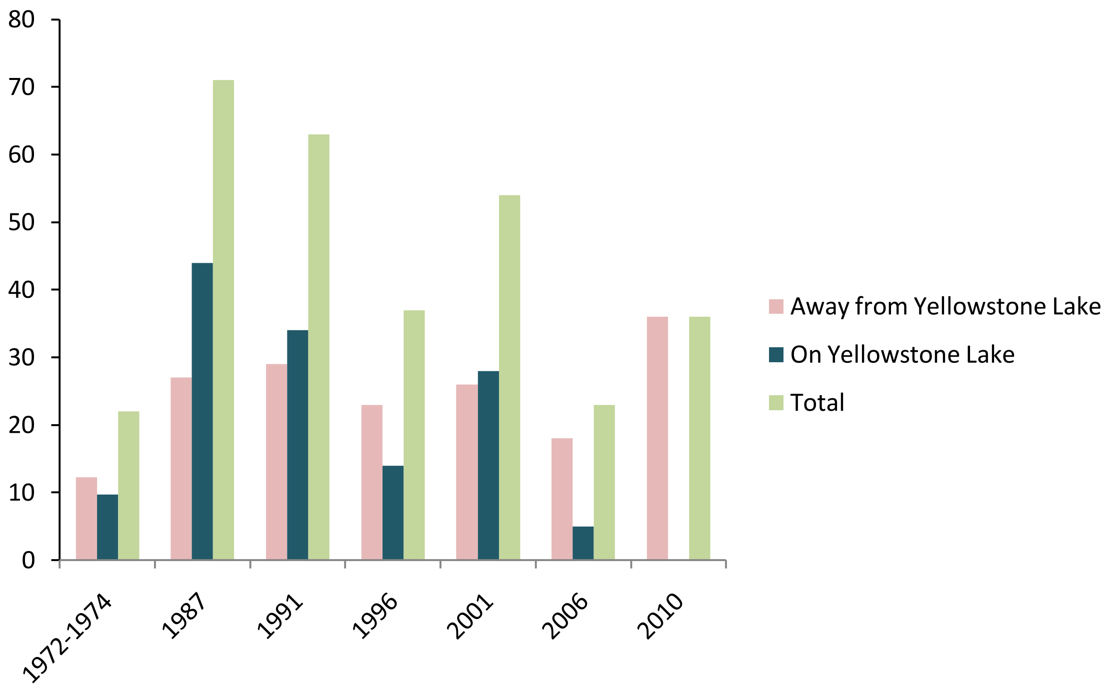

Fig. 6: Young fledged on and away from Yellowstone Lake for the period 1987-2010. The counts for 1972-74 are average numbers for this period (Swenson 1975).

Correlations between the osprey population and the cutthroat trout population

I found a significant correlation between the number of active osprey nests in YNP and the in-lake index of the cutthroat population in Yellowstone Lake when adding more than a 3-year time lag ($p < 0.05$). The best correlation was found by adding a 6-year time lag (Pearson correlation value: 0.97; n=11, Fig. 7). There was also a correlation between number of young fledged and the in-lake cutthroat population. This correlation was significant even without adding any time lag (p=0.045), but became more significant by adding 2 to 6 years of time lag ($p < 0.005$), with a peak at 3 years (Fig. 8).

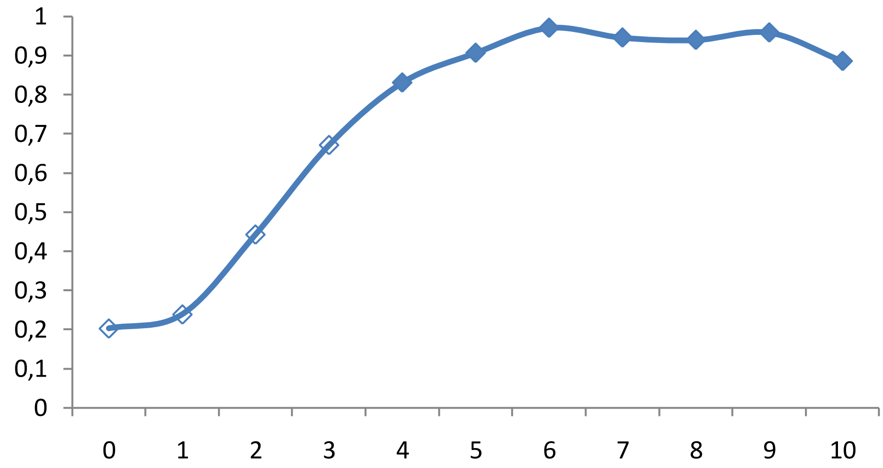

Fig. 7: Change in Pearson correlation coefficients between number of active osprey nests in YNP and the in-lake index of the cutthroat population in Yellowstone Lake, with added time lags of 0-10 years. Open data points indicates non-significant correlations (p>0,05).

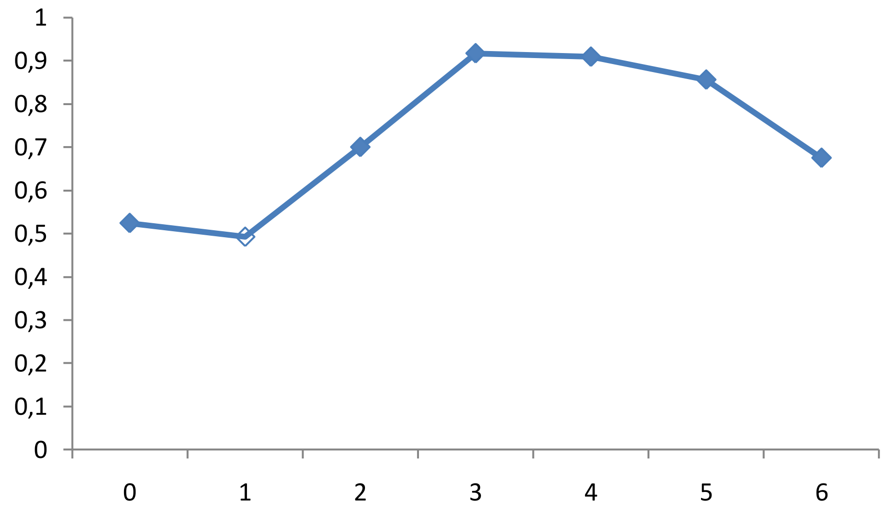

Fig. 8: Change in Pearson correlation coefficients between number of fledged young in YNP and the in-lake index of the cutthroat population in Yellowstone Lake, with added time lags of 0-6 years. Open data points indicates non-significant correlations (p>0,05).

Discussion

Feeding habits

None of the ospreys observed on Yellowstone Lake during the summer 2010 were observed foraging on the lake. This strongly suggests that the ospreys went elsewhere to forage. This result is in contrast to the observations of Swenson (1975), who reported foraging activity throughout Yellowstone Lake for a total of more than 400 min per season during his field work in 1973 and 1974.

Observations from the nests in West Thumb showed that the ospreys were flying away from the lake on several occasions. The ospreys were not observed bringing fish back to the nest, and no remains of fish bones were found underneath the nest trees. Based on those observations I suspect that the ospreys were flying to lakes and rivers near Yellowstone Lake to feed. Because the reproductions were unsuccessful, the fish were probably eaten away from the nest. Swenson (1981) found that ospreys nesting in the Grand Canyon were primarily foraging on Yellowstone Lake and Grebe Lake 4.5, km and 5.6 km from the nests, respectively. Within such flying distances, both Shoshone Lake and Lewis Lake could be reached from the nests in West Thumb. Both the Upper Yellowstone River and Heart Lake are within reach for ospreys nesting on the Promontory between the South Arm and Southeast Arm.

The observation that the ospreys fly great distances to forage suggests that close foraging sites are not the only factor in the choice of nesting sites. Other factors can be e.g. nesting tree characteristics and weather conditions (Edwards & Collopy 1988; MacCarter & MacCarter 1979; Swenson, J. E. 1979). However, the long foraging distances can affect foraging effectiveness and may have contributed to the reproduction failure on Yellowstone Lake. Disturbances by humans can also play a part in the reproduction outcome (MacCarter & MacCarter 1979; Swenson, J.E. 1979). Both nests in West Thumb were located close to a heavily trafficked road and the nest with the most observed activity was just 60-70 m from a popular viewpoint of the lake. Traffic or human activity did not seem to affect the osprey’s behavior however.

Nest distribution and reproduction success

Continuous data series on distribution and reproduction in YNP from the last three decades would have been optimal for analyzing trends and changes in the osprey population. However the NPS could only provide me with data on nest distribution and reproduction from 1987 to 2010 at five-year intervals. Natural variations between years will thus not be considered. I realize that this limits the strength of my analyses, but even without continuous data series, I consider the trends shown in the available data to be clear enough to base the analyses upon them.

Skinner (1917) estimated the number of breeding pairs of ospreys in Yellowstone to be 120 during his study. This indicates that the historical numbers of ospreys in YNP probably was higher than it has been at least the last 40 years. Swenson (1979) estimated the total population to be about 45 pairs. In 1994 the number were as high as 100 nesting pairs in YNP (McEneaney 2007), but since year 2000 the total population has declined from 96 pairs to only 30 in 2010. There was a significant decrease in the number of active nests, reproductive success, and number of fledged young at Yellowstone Lake from 2001 to 2006. Other reports and observations also indicate that the osprey population on Yellowstone Lake was doing well until the start of the new millennia (Baril et al. 2010; Baril 2009; McEneaney 2005). One reason for the changing situation between 2001 and 2006 may be the fire on Frank Island in 2003. This island used to be a major nesting place for ospreys on the lake, with as many as 25 nesting pairs in 1994 (McEneaney 2007). After the fire the ospreys have not reestablished on the island and in 2010 no active nests were observed on Frank Island.

All reproductive parameters and the number of nesting birds have increased if the average numbers for the years 1987, 1991, 1996, 2001, 2006 and 2010 are compared with the average numbers from 1972 to 1974; The average number of nesting pairs of ospreys in YNP has increased from 36 to 61, the number of successful nests has increased from 15 to 27.8, nest success has increased from 41 to 49, and the average number of young fledged has increased from 22 to 47.3. Such a comparison does not necessarily give an accurate picture of the development in the Yellowstone osprey population, but an increase in the osprey population during the last three decades has also been found elsewhere in the North America (Harmata et al. 2007; Henny et al. 2008a; Henny et al. 2008b; Monson 1996). In parts of the upper Missouri River, Montana, Harmata et al. (2007) shoved an increase in nest density (pairs per km) as high as 88% from 1981-1982 to 1998-1999. Henny (2008a) reported an increase of nesting pairs in an area in northwestern Mexico of 81% from 1977 to 2006. In another study on the Columbia River, Henny found an annual increase in an osprey population of 13.7% per year from 1997 to 2006 (Henny et al. 2008b). In the same study he found that the concentration of most organochlorine pesticides (OCs) in osprey eggs was significant lower in 2006 than in 1997. There are many studies regarding the reproductive effects of high concentrations of OCs and other bioaccumulative contaminants in osprey eggs (see Grove 2009). The insecticide DDT was banned in the US in the early 1970s. Since then the concentration of DDE (the breakdown product of DDT), known to cause thinner eggshells and reproductive failure in raptor populations, has declined. This has facilitated the recovery in many osprey populations in North America (Ewins 1994). A decline in use of DDT may be one of the reasons for the increase in the osprey population in YNP. DDT was used for spruce budworm (*Choristoneura fumiferana*) control in YNP the 1950s and in surrounding National Forests as late as in 1963 (Swenson et al. 1986). The ospreys nesting in YNP was probably also affected by DDT and other toxic contaminants in their wintering grounds.

The productivity in the Yellowstone osprey population has been on average 0.78 young per active nest for the lasts two decades. This is below what required to keep the population stable, which is between 0.95 and 1.30 young per nesting female (Henny & Wight 1969). The osprey population in the park can thus be characterized as a sink, defined as a population where death rate is greater than the birth rate. In contrast, a source is a population where the birth rate exceeds the death rate (Pulliam 1988). Without immigration from source populations the sink would decline toward extinctions. Harmata et al. (2007) found that it was that the productivity of the osprey population on the Missouri River was higher during the 1990s than the minimum estimate to keep the population stable. Immigration from this and other adjacent osprey populations have probably maintained the population stability in YNP. The low productivity in the Yellowstone osprey population can partly explain why the nests on Yellowstone Lake have not been recolonized. Because there is no surplus reproduction, there would be enough available nest sites in more optimal habitats, and first-time breeders would not need to choose a nest on Yellowstone Lake, where there apparently is a lack of food resources.

Change in fish community and effects on the osprey population

It is difficult to determine when the lake trout population reached a level high enough to affect the ospreys. Gresswell (2009) wrote that "Currently, there is no statistically robust monitoring program for evaluating distribution and relative abundance of lake trout in Yellowstone Lake..... Yellowstone cutthroat trout and lake trout have been collected lakewide with hydroacoustic equipment over multiple years, but to date, analysis is incomplete". Lack of knowledge about the distribution of lake trout also makes it difficult to determine if there are areas of the lake where the impact of the lake trout has been less severe, and the cutthroat is still thriving. Gillnetting and other methods have revealed the existence of lake trout throughout most parts of the Lake. In 2004 probable spawning locations in the Southeast Arm were found by use of an airborne lidar (optical remote sensing technology) (Shaw et al.). In This remote part of the lake, lake trout were not known to exist earlier. Evidence of a thriving lake trout population in this part of the lake is supported by my own experiences from my fieldwork.

Monitoring Lake has documented a dramatic decline in the population of the cutthroat trout in Yellowstone since the late 1980s (Koel 2010; Koel 2007). Monitoring of spawning migration traps in the Yellowstone Lake tributary Clear Creek has shown a decline in the number of upstream migrating cutthroat trout from nearly 55,000 in 1988 to only 538 in 2007 (Koel 2010). In Bridge Creek, another tributary to Yellowstone Lake, Koel (2005) reported an annual decline of spawning cutthroat of more than 50% per year. The cutthroat population is also monitored by an in-lake fall netting assessment. The average catch per net in this assessment has decreased from around 16 in 1994 to around 5 in 2006, but increased to about 9 in recent years (Koel 2010). Since the in-lake gillnetting also captures immature cutthroat trout in the size-range preferred by the ospreys, the catch statistics from the fall netting assessment were most relevant for my analyses.

The significant correlations between the cutthroat trout population (average catch per net) and both nesting pairs of ospreys and number of young fledged, suggests that the decline the in cutthroat trout population in Yellowstone Lake has affected the osprey population in a negative way. The best correlation between the nesting osprey population and the cutthroat trout population occurred with a time leg of 6 years. It is reasonable to suppose that it takes some years before the osprey population responds to a decline in the cutthroat trout population. Assuming an osprey population without immigration and emigration and where the ospreys fledged within a territory will return to this territory to breed, a reduction in the number of fledged young in year *1*, will first affect the number of breeding pairs after *n* years, when the fledged young in year *1* reach the age of maturity. By Henny and Wight (1969) the age of the first time breeders, found to usually be 3 years. Counting for the time it takes before a decreasing cutthroat population affects the reproduction outcome and the time it takes before a reduced reproduction led to a reduced number of nesting pairs, a significant correlation between number of cutthroat and number of nesting birds after a time lag of 4 years or more seems reasonable. It was also expected that the years of time lag needed to get a significant correlation was fewer for the reproductive outcome, than for the number of nesting pairs. A shortage of food will naturally first affect the number of young fledged before it affects the number of nesting birds. According to Henny and Kaiser (1996) ospreys remain faithful to their nesting territories after first-time nesting. This can partly explain why some ospreys continues to nest on the lake even thou the food resources are too scarce to get a successful reproduction.

Management recommendations

The only way to restore an ecological balance in the Yellowstone Lake ecosystem is probably through removal of the lake trout. A lake trout removal program was initiated after the discovery of lake trout in 1994, and the catches have increased steady since then. In 2008 more than 76,000 lake trout were removed from Yellowstone Lake (Gresswell 2009; Koel 2010). Despite the high suppression efforts, the spawning cutthroat trout population still has not shown a significant positive response to the lake trout removal. A review panel was constituted in 2008 to evaluate the lake trout removal program.

This review panel recommended intensified lake trout suppression, enhanced monitoring of the cutthroat trout population, initiation of a statistical robust lake trout monitoring program, and development of a lake trout suppression plan to increase the effectiveness of the lake trout removal efforts (Gresswell 2009).

To gain more information on the foraging habits of the Yellowstone osprey population, it is necessary to consider other methods than just visual observations. My experiences showed me that monitoring of nests is not only very time consuming but also an ineffective method. One way to find out where the ospreys are foraging could be to use GPS-telemetry. GPS- tracking could be used to calculate foraging distances and to determine which lakes and rivers are most utilized by the ospreys. A relevant study could be to see how foraging distances affect productivity. I think it also would be of interest to conduct a more thorough monitoring of the active nests in South and Southeast Arms. Due to logistic problems and closure of areas due to bear restrictions, little information was gained from those nests during my fieldwork.

I strongly recommend a continuing monitoring of the osprey population in YNP. If the lake trout suppression is shown to be effective, with an increase in the cutthroat trout population as result, I think it would be of great interest to compare this increase with number of nesting pairs and productivity of the ospreys nesting on the lake.

The results from this study have suggested serious ecological impacts by the introduction of lake trout on ospreys on Yellowstone Lake. The osprey is probably only one of many species affected by the declining cutthroat population, and more research is needed to see the total impact to the Yellowstone Lake ecosystem. Experience from YNP has shown that, despite strong legislation and heavy suppression efforts, it is difficult to remove introduced species once they have become established in a suitable environment. This illustrates the global problem with introduction of nonnative species into new habitats; once they are there, they can do much harm on the natural ecosystem and they are often difficult to eliminate. I hope that my study and knowledge gained from the situation on Yellowstone Lake, can contribute to science and management issues regarding alien species, both in YNP and elsewhere in the world.

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