ASSESSMENT OF LAKE TROUT REFUGE EFFECTS ON
TRENDS IN RELATIVE ABUNDANCE OF SELECT NATIVE FISH SPECIES IN THE
APOSTLE ISLANDS REGION, LAKE SUPERIOR

By

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ABSTRACT

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The lake trout refuges in the Apostle Islands region of Lake Superior are analogous to the traditional concept of a marine protected area. These refuges closed to most forms of fishing have been implicated as one of several management actions leading to the successful rehabilitation of Lake Superior stocks of lake trout (*Salvelinus namaycush*). To further investigate the ecological significance of these two refuges on both target and non-target species, I analyzed fishery-independent survey data collected by the Wisconsin Department of Natural Resources since 1982 and evaluated trends in mean catch of lake trout, lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*) sampled inside versus outside of refuge boundaries. I found that lake trout relative abundance was higher inside the refuges and also increased at a greater rate inside the refuges, where lake trout fishing was prohibited, than outside. The annual relative abundance of lake whitefish was higher in areas outside of the refuges. However, the rate of increase in lake whitefish relative abundance was greater inside refuge boundaries, which was indicative of a refuge effect. Analysis of relative abundance of cisco, a potential prey item of lake trout, did not demonstrate significant trends in either area. Overall, this study highlights the potential importance of the refuges for enhancing populations of species beyond those that were the original target of the refuges, as demonstrated by the changing relative abundance of lake whitefish. Improved understanding of refuge effects on populations of Great Lakes fishes is therefore valuable to inform future fisheries management.

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INTRODUCTION

The declining health of aquatic ecosystems, loss of aquatic biodiversity, and the

overexploitation and collapse of many of the world's fish stocks are pressing issues of concern

requiring a multi-faceted response, including the use of marine protected areas[1] (MPAs)

(Jackson et al. 2001; Pauly et al. 2002; Roberts 2003; Taylor et al. 2011; Worm et al. 2006;

Worm et al. 2009).   These areas have been gaining worldwide attention for their role in

facilitating recovery of impaired ecosystems and biota, protection from and mitigation of

anthropogenically-induced threats to habitats and resources, and maintenance of ecosystem

services, such as those linked to fisheries, recreation, cultural heritage, and educational

opportunities (Jones 1994; NRC 2001; Halpern and Warner 2002; Lubchenco et al. 2003; Sobel

and Dahlgren 2004; Roberts et al. 2005; Gray 2010). Protected areas where extraction of aquatic

life is prohibited, commonly referred to as reserves, can "provide insurance against uncertainty"

related to traditional approaches to fisheries management and conservation (NRC 2001). This

uncertainty is a reflection of the inherent spatial and temporal variability of fish stocks and

environmental measures used to develop assessments that inform fisheries management

decisions, such as harvest controls or habitat enhancements (Lauck et al. 1998; NRC 2001).

However, there are also political, economic, social, cultural, and ecological costs associated with

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[1] "Marine Protected Area" is often used as a generic umbrella term for any aquatic zone that has
some level of designated protection, from no-take areas to sites zoned for multiple uses.
Therefore, a variety of other terms are used according to the level of protection and governing
body, (e.g., refuges, reserves, conservation areas, sanctuaries, etc.). According to the Natural
Resources Council (2001), an MPA is defined as a, "geographic area with discrete boundaries
that has been designated to enhance the conservation of marine resources. This includes MPA-
wide restrictions on some activities, such as oil and gas mining, and the use of zones, such as
fishery and ecological reserves, to provide higher levels of protection." An additional definition
is, "any area of intertidal or subtidal terrain, together with its overlying water and associated
flora, fauna, historical and cultural features, which has been reserved by law or other effective
means to protect part or all of the enclosed environment," (Kelleher and Kenchington 1992).

reserves that can prompt controversy (Jones 2002; Sanchirico et al. 2002; Hilborn et al. 2004; Jones 2006; Agardy et al. 2011). Nevertheless, the focus on MPAs in approaches to coastal systems management in the United States is likely to further increase following recent legislation in support of coordinated placement of MPAs to maximize benefits across the nation's aquatic environments, including the Great Lakes (National MPA Center 2008).

Aquatic protected areas (APAs), which are analogous to MPAs but also encompass freshwater environments, have been established for various purposes throughout the Great Lakes region (Hedges et al. 2010; Hedges et al. 2011). One such example of these APAs exists in the form of state-managed refuges for lake trout (*Salvelinus namaycush*) rehabilitation. Stocks of this primary, native piscavore collapsed across the Great Lakes by 1950 because of overexploitation, sea lamprey (*Petromyzon marinus*) predation, and habitat degradation (Krueger et al. 1995; Hansen 1999). The Great Lakes Fishery Commission subsequently facilitated interagency and international research and management efforts to rehabilitate lake trout stocks through a variety of fish conservation programs and activities (Krueger et al. 1995; Hansen 1999). The refuges, closed to year-round lake trout harvest and identified as sites for intensive stocking efforts, were specifically zoned according to traditional knowledge of spawning reefs. It was assumed that these locations contained better spawning habitat than other regions of the lakes and thus would have higher adult spawner abundances, thereby resulting in an increased likelihood of stock recruitment success and wild fish production (Swanson and Swedberg 1980; Stanley et al. 1987; Hansen et al. 1995; Holey et al. 1995; Schram et al. 1995; Hansen 1999).

Extensive long-term monitoring near and in these refuges has been completed to assess progress toward lake trout rehabilitation goals (e.g., Schram et al. 1995). Analyses in Lake Michigan (e.g., Madenjian and DeSorcie 1999) and Lake Huron (e.g., Madenjian et al. 2008) can be viewed as implicating varied conclusions regarding effectiveness of refuges for improving

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lake trout stock abundance, survival, growth, spawning success, and natural reproduction. Contrary to efforts in Lakes Michigan and Huron, advancements toward successful lake trout rehabilitation in Lake Superior have been more consistently noted (Hansen *et al.* 1995; Schram *et al.* 1995; Linton *et al.* 2007). With the exception of attention to historical shifts in fish community composition in regions of the Great Lakes that included refuges (Eshenroder and Burnham-Curtis 1999; Kitchell et al. 2000; Bronte et al. 2003), previous studies involving Great Lakes APAs have not explicitly assessed changes in preyfish community composition or invertebrates supporting the local foodweb as a means to evaluate the refuges' impacts on lower trophic levels within the refuge or surrounding region. Given the body of evidence showing that fishing closures can have indirect, and even trophic cascading, effects (Pinnegar et al. 2000; Sobel and Dahlgren 2004; Baskett et al. 2007; Babcock et al. 2010), it warrants investigation to see if the refuges in the Great Lakes are impacting fish species beyond lake trout that serve an important role in fish community structure, function, and productivity. The goal of this research was to therefore evaluate the potential effects of refuges on abundances of a suite of Great Lakes fishes, whether these effects be directly related to mechanisms involving restricted fishing mortality or indirectly related through species interactions on target and non-target fish species. The selected species for this evaluation include lake trout, lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*).

Background

Use of reserves as fisheries management tools

Beyond their potential benefits for habitat protection and biodiversity conservation, the role and efficacy of reserves (no-take MPAs) in fisheries management is frequently discussed in

the literature (Roberts et al. 2001; Gell and Roberts 2003; Halpern 2003; Hilborn et al. 2004; Sale et al. 2005; Halpern et al. 2010; Gaines et al. 2010; Vandeperre et al. 2010; Worm et al. 2009). Implementation of these reserves can serve a role in a precautionary approach to fisheries management (Lauck et al. 1998) in which they are meant to provide "insurance" against potential errors in conventional management – essentially providing a buffer in the face of uncertainties in stock assessments and associated harvest regulations (Allison et al. 1998; NRC 2001; Sobel and Dahlgren 2004). Increased fisheries yields in regions surrounding these areas protected from harvest is a primary and active potential benefit of well-designed reserves (Roberts et al. 2001; Gell and Roberts 2003; Sobel and Dahlgren 2004). Larval export from reserves increases productivity through replenishment of recruits in external fishable areas (Halpern et al. 2004; Pelc et al. 2010). The other primary mechanism by which reserves can bolster fish populations outside of refuge boundaries is known as the spillover hypothesis, which asserts that fish will likely move from areas of higher density within reserves into adjacent areas (Russ and Alcala 1996; NRC 2001), as evidenced by numerous studies in marine systems (Russ and Alcala 1996; Halpern et al. 2010; Vandeperre et al. 2010). In addition, reserves can support increased ecological resilience by maintaining fish stocks of sufficient diversity to withstand harsh environmental and anthropogenic perturbations (Babcock et al. 2010). Reserves can also serve as a reference site in research and monitoring aimed at increased understanding of fish population dynamics (NRC 2001; Hilborn et al. 2004; Guidetti and Micheli 2011).

However, despite the potential ability of reserves to enhance sustainability of fisheries through improved habitat and increased fish community diversity, population abundance, production, and resilience, assessment of the efficacy of reserves is complicated (Gell and Roberts 2003; Sale et al. 2005). Potentially confounding issues include deleterious effects associated with environmental degradation of aquatic habitats caused by changes in climate,

pollution pressure from anthropogenic sources, or introduction of invasive species that increase competition or predation with native species (Hedges et al. 2010). All such factors affect the viability of fish stocks, thereby obscuring analyses aimed at determining whether protected areas are serving their intended purpose. In addition, attempts to evaluate reserve function can be complicated if the original design of the reserve improperly accounted for the specific dynamics of the local system or focal species (Botsford et al. 2003; Sale et al. 2005), or if inappropriate experimental designs were used to analyze existing reserves (Willis et al. 2003b; Claudet and Guidetti 2010). Additionally, Hilborn et al. (2004) presented a convincing case against blind acceptance that all potential fisheries benefits associated with reserves would consistently occur. For example, to be effective at multiple levels (e.g., economic and ecological) that directly affect fisheries, a reserve must provide sufficient fishable biomass to the outside area at a sustained rate that outweighs the expense of the closure on local fisheries (Hilborn et al. 2004; Sale et al. 2005). The protected source population must also be able to withstand the effects of net exports of fish to surrounding areas when faced with long-term fishing pressure outside reserve boundaries (Sale et al. 2005). Subsequent displacement of fishing effort caused by establishment of no-take areas can have both ecological effects on neighboring fish populations and economic effects on fishermen and local communities (NRC 2001; Halpern et al. 2004; Hilborn et al. 2004). Additionally, indirect effects of protecting predatory species from harvest can negatively affect prey species (Babcock et al. 2010). Therefore, consideration of the life history and ecology of all affected species, as well as the extent of adjacent fishing effort, is important when assessing use of a reserve over other fisheries management tools (Gell and Roberts 2003; Hilborn et al. 2004; Botsford et al. 2009).

Given the complexity of reserve function and evaluation, the efficacy of reserves for fisheries sustainability is controversial. This is especially true for fisheries, which may be

thought of as a "common" and open resource (Gordon 1954). Ultimately, the collective goal

associated with reserves is "sustainability at the lowest cost (or maximum benefit)" (Halpern and

Warner 2003). However, stakeholders may differ in their opinion of what should be sustained

and what constitutes an improvement or degradation of environmental, economic, social, or

cultural conditions (Halpern and Warner 2003). Therefore, there are serious and ongoing

debates between those who believe the benefits of reserves outweigh the costs, and those who are

not convinced of the potential effectiveness of these areas for increased fisheries productivity.

Ultimately, opposing viewpoints must be acknowledged and considered, while communicating

the most current science during dialogs surrounding reserve implementation and evaluation

(Jones 2002; Agardy et al. 2003; Halpern 2003; Pajaro et al. 2010).

APAs in the Great Lakes

Fewer APAs are located in the Great Lakes than in marine waters of the United States

(i.e. not including the use of temporal closures, or fishing seasons). This situation may reflect

the proportionally limited worldwide focus on protected areas in fresh waters relative to those in

marine environments (Abell et al. 2007). In large lakes, such area-based protection is also often

associated with shorelines of terrestrial protected areas (Hedges et al. 2010). According to

NOAA's MPA Inventory (as of April 2011), the U.S. portion of the Great Lakes contains 93

APAs (NOAA 2011b). Of these, six are official members of the National System of MPAs, a

partnership of self-nominated sites that adhere to a defined set of national conservation

objectives. However, few APAs in the Great Lakes could be considered equivalent to the

concept of no-take MPAs (reserves) (Hedges et al. 2010; Hedges et al. 2011; NOAA 2011a).

The lake trout refuges of the upper Great Lakes may be the closest analog to marine

reserves for their purpose in promoting fisheries restoration through exclusion of fishing

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mortality, particularly those in Lake Superior, due to their use of no-take zones within refuge

boundaries. Refuges in Lakes Superior, Huron, and Michigan are closed to recreational and

commercial harvest of lake trout (Stanley et al. 1987; MDNR 2011; WDNR 2011), while those

in Lake Michigan and Lake Huron do allow harvest of other species (MDNR 2011). Restrictions

generally extend to all species in Lake Superior refuges except in specially designated zones for

certain fisheries during limited timeframes. Despite these exceptions, the existence of zones that

are completely closed to fishing within the refuges makes them a prime study site for further

evaluation of reserves in the Great Lakes, because changes in fish abundance can be studied in

the absence of fishing mortality.

Evaluations of lake trout populations in and around these refuges have thus far

demonstrated varied levels of progress toward rehabilitation. For instance, studies involving the

lake trout refuges in Lake Michigan (Holey et al. 1995; Fabrizio et al. 1997; Madenjian and

DeSorcie 1999; Bronte et al. 2007; Madenjian and Desorcie 2010) failed to demonstrate

evidence of lake trout reproduction, a necessary factor for population rehabilitation. However,

lake trout spawner densities sometimes associated with refuges were theoretically adequate for

reproduction, thus indicating other factors independent of fishing mortality (such as limited

survival of stocked eggs and fish, sea lamprey predation, competition with exotic fish species, or

degraded habitat) limited lake trout recruitment (Holey et al. 1995; Madenjian and DeSorcie

1999; Bronte et al. 2007). In another study, lake trout were observed spawning on a deep,

offshore reef complex (Janssen et al. 2006) that includes the Midlake Refuge. This finding could

be taken to imply refuges serve a purpose in Lake Michigan when established to protect actively

spawning adults, despite the other factors confounding restoration efforts. Similarly, Bronte et

al. (2007) recommended stocking continue at offshore sites with good spawning habitat and

limited fishing and sea lamprey mortality; these conditions theoretically persist within Lake

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Michigan's refuges. However, recent declines in lake trout abundance since the 1990s within Lake Michigan's Northern Refuge may be linked to reduced stocking levels, with populations also affected by the possibly contrasting effects of increased sea lamprey mortality and reduced harvest pressure outside the refuge (Mandenjian and Descorcie 2010). This emphasis on other limiting factors could also be interpreted to mean the protection from fishing mortality within the refuge did not play a significant role in efforts toward rehabilitation of the lake trout stock in the area.

In Lake Huron, theoretically adequate abundances of spawning lake trout developed, but recruitment of wild fish was limited (Madenjian et al. 2004; Madenjian et al. 2008). However, some incidences of natural reproduction proved promising for rehabilitation efforts (Desorcie and Bowen 2003), and analysis of rebounding populations near a refuge in the Canadian waters of Lake Huron suggested the refuge made a contribution to this recovery (Reid et al. 2001). Also similar to analyses conducted on Lake Michigan (e.g., McKee et al. 2004), researchers focused on the stocking success of different lake trout strains in Lake Huron refuges (Madenjian et al. 2004; Roseman et al. 2009), as opposed to explicit evaluation of the refuges themselves. Some ultimately asserted that management actions, such as reductions in fishing effort and designation of the refuges, played a role in promoting lake trout rehabilitation by limiting fishing mortality despite the fact that other factors (such as sea lamprey predation) continued to delay full recovery (Madenjian et al. 2008). Others further reiterated that the refuges should be maintained as stocking sites (Madenjian et al. 2004) and ultimately for their role in protecting spawning lake trout (Desorcie and Bowen 2003).

The existence of naturally reproducing, self-sustaining populations in Lake Superior (Bronte et al. 1995a; Hansen et al. 1995; Schram et al. 1995; Linton et al. 2007) highlights the importance of the affiliated refuges for lake trout rehabilitation. Initial research completed by

Swanson and Swedberg (1980) asserted that spawning on the reef within the Gull Island Shoal Refuge (Figure 1) had immediate potential to improve lake trout stock conditions in the absence of fishing pressure in the years after its establishment. Evidence of this success was demonstrated by 1990 through existence of a truncated lake trout age structure in the non-protected inshore portions of the Apostle Islands, as compared with a much wider distribution within offshore protected areas (Hansen et al. 1996). This greater span of age groups and presence of older age classes is indicative of a more reproductively mature and productive stock, in which individuals have survived longer, presumably due to the absence of fishing pressure.
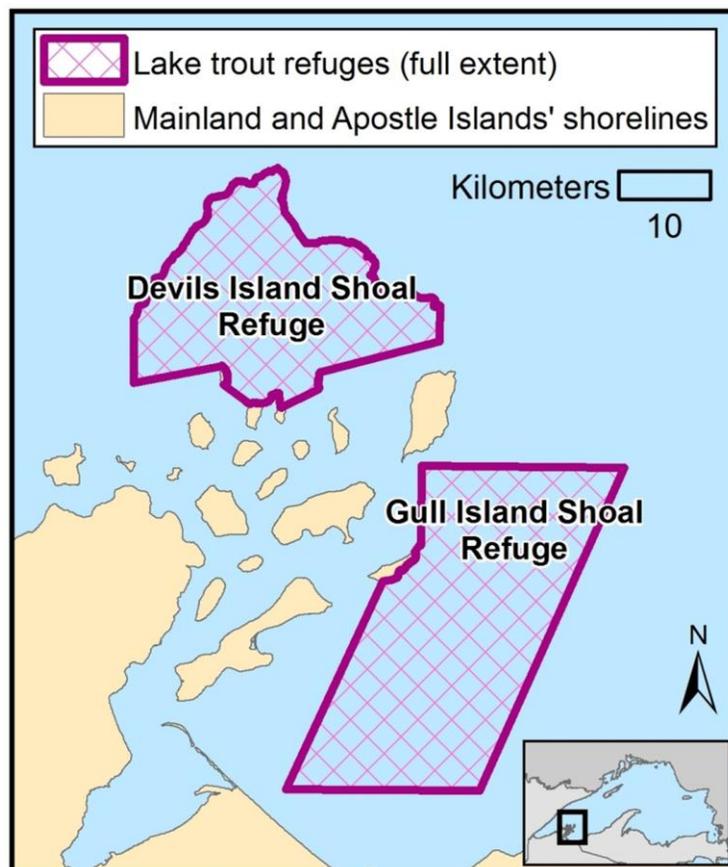
FIGURE 1. Lake trout refuges in the Apostle Islands region. (Inset: Lake Superior). Full refuge extent is indicated by the purple line surrounding cross-hatching. Detailed information about base layer data sources is available in the Appendix. *For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.*

The altered age structure also implied that lake trout subject to greater exploitation in non-protected inshore areas had faster growth rates than those in the refuges (Hansen et al. 1996). Additionally, Schram et al (1995) asserted that the lack of substantial fishing effort in Michigan waters east of the Gull Island Shoal refuge during the 1970s and early 1980s may have further contributed to the presumed success of the refuge by essentially increasing the "protected" area's extent. In other demonstrations of potential correlations linked to this refuge, in particular, Pollock et al. (2007) noted that estimates of lake trout survival were higher after refuge implementation and also higher inside refuge boundaries than outside. Fabrizio et al. (2001) also noted a reduction in lake trout growth rates in the years after refuge establishment, but could not distinguish whether the change was due to density-dependent processes linked to reduced prey availability or to other density-independent environmental factors. However, in a study of lake trout population dynamics from 1988 through 1995, Corradin et al. (2008) found evidence of density-dependent effects, such as reduced recruitment rates potentially driven by intra-specific competition and limited food availability, which are indicative of a population that has recovered to the point of reaching carrying capacity. It is also consistent with similar density-dependent feedback loops demonstrated in other analyses of marine reserves (e.g., Sánchez Lizaso et al. 2000).

Several additional aspects of these lake trout refuges make them especially suitable candidates as a study site for an APA evaluation in the Great Lakes. The relatively long-term nature of these refuges (having been in place for decades) and associated monitoring have led to development of large datasets allowing for tracking of changes in fish abundance and growth parameters for a suite of fish species caught in assessment nets. Also, the perceived success of these refuges, particularly in Lake Superior, toward lake trout rehabilitation goals makes them noteworthy for their role as an APA for mobile species (Hedges et al. 2010) that may be more

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difficult to conserve owing to the relatively larger proportion of time such species may spend outside of reserve boundaries.

Lake trout

Lake trout, the focal species of these refuges in the Great Lakes, are a native apex predator and historically inhabit the highest trophic level in Lake Superior (Kitchell et al. 2000). Juvenile lake trout predominantly feed on invertebrates and adult lake trout historically preyed primarily upon native *Coregonus spp.* (Hansen et al. 1995). However, the establishment of exotic rainbow smelt (*Osmerus mordax*) coupled with declines in cisco (Selgeby 1982) resulted in a shift in diet composed predominately of rainbow smelt in the 1980s and 1990s (Gorman 2007; Ray et al. 2007). Changes in fish community composition over the last several decades have included fluctuations in rainbow smelt abundance and increased abundances of cisco; the latter of which have been relied upon more heavily as a lake trout prey item since the 1990s (Bronte et al. 2003; Gorman 2007; Ray et al. 2007).

In general, lake trout inhabit depths shallower than 73 meters (Hansen et al. 1995) and according to records compiled by Dryer (1966), have historically been found in depths ranging 18 – 71 meters, with the highest abundances sampled at 36 – 53 m. Deepwater morphotypes (siscowets) can be found at depths ranging 91 – 183 m (Eschmeyer and Phillips 1965). Lake trout spawn in the fall, usually from October through early November, on rocky reefs and shoals in waters shallower than 36 m (Eschmeyer 1955), however more recent studies have only observed evidence of spawning on reefs shallower than 18 m (Marsden et al. 1995). Siscowets may spawn in other times of year ranging from June to November (Eschmeyer 1955) and are prompted by the cooler temperatures found in deeper waters below the thermocline (Marsden et al. 1995). A study completed by Bronte (1993) also found evidence of April spawning by

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siscowets immediately north of the Apostle Islands, including locations that appear to be in or near the Devils Island Shoal Refuge (Figure 1), therefore indicating that this refuge can serve a purpose in protection of spawning fish outside of the normal lean lake trout spawning season.

Wild lake trout also appear to show some level of spawning site fidelity and return to the same reefs to spawn in subsequent years, as opposed to stocked fish that do not return as consistently to the same sites, especially when reefs are located offshore (Eschmeyer 1955; Rahrer 1968; Krueger et al. 1986). The extent of wild lake trout movement away from spawning sites depends on the time of year and can range from eight to 163 kilometers (Rahrer 1968; Kapuscinski et al. 2005). In Lake Superior, the vast majority of adults remained within 80 km of tagging sites located within refuge boundaries (Rahrer 1968). In the WI-2 management unit of the lake (Figure 2) that contains the refuges, lake trout movements, on average, ranged from
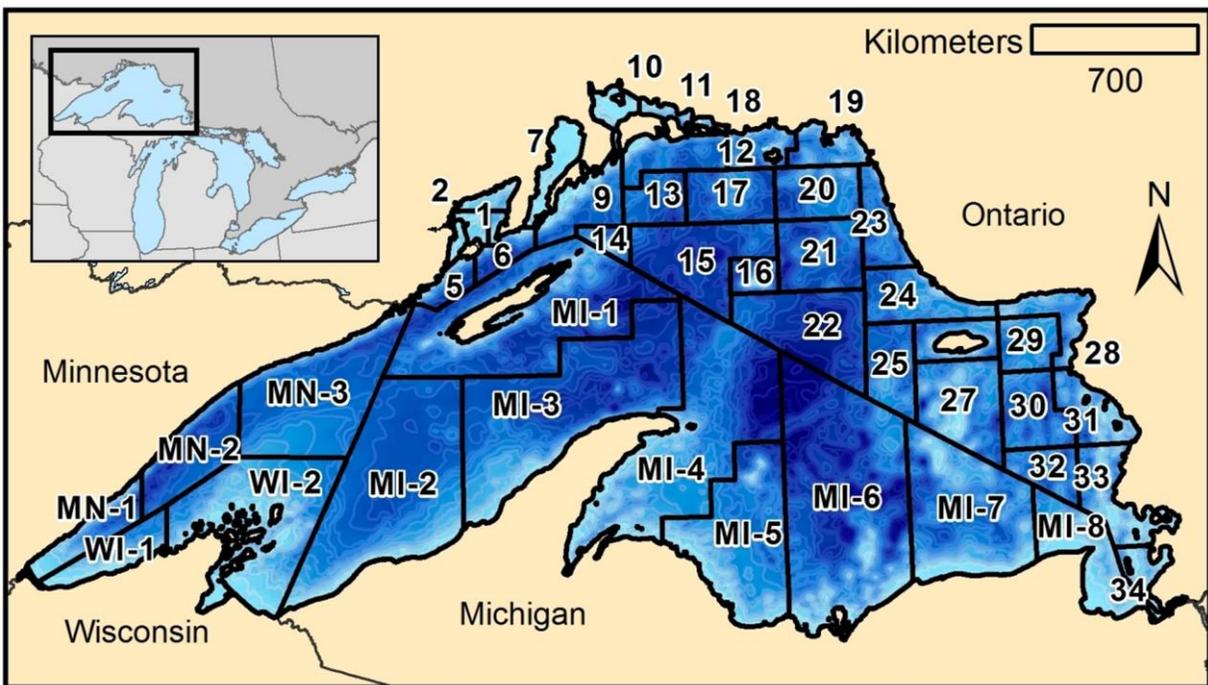
FIGURE 2. Lake Superior fishery management units. (Inset: Laurentian Great Lakes). The study region is located within the WI-2 management unit, which also encompasses the Apostle Islands. Blue shading denotes bathymetry (darker = deeper). Detailed information about base layer data sources is available in the Appendix.

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44.28 km during the non-spawning season to 9.46 km during spawning times (Kapuscinski et al. 2005).

Once an abundant component of the Great Lakes fishery, lake trout, along with lake whitefish and cisco, supported fisheries dating back to before European settlement (Hansen 1999). A long period of overfishing during the 1930s and 1940s combined with invasion and subsequent predation by sea lampreys and, to some extent, deleterious effects of contaminants and habitat degradation, were said to be among the primary likely causes for lake trout stock collapses across the Great Lakes region by the 1950s and 1960s (Hansen 1999). In Lake Superior, the majority of lake trout spawning stocks were depleted during the 1950s due primarily to continued sea lamprey predation, as well as pressures from fisheries harvest (Pycha and King 1975), with numbers reaching as low as one fish per 1000 m of gillnet by 1960 in the Apostle Islands region (Swanson and Swedberg 1980). In the early 1960s, Gull Island Shoal included one of the only remaining stocks of naturally reproducing lake trout in the Apostle Islands, making it an obvious choice for involvement in subsequent rehabilitation efforts (Swanson and Swedberg 1980; Pollock et al. 2007).

The road to recovery has been a long and intensive process. Key factors that likely contributed to increases in lake trout populations in Lake Superior included a combination of sea lamprey control efforts beginning in the late 1950s, lake trout stocking, and harvest regulations (Hansen et al. 1995). Stocking began in 1952 in Wisconsin waters (Lawrie and Rahrer 1973), and the commercial fishery was closed in 1962 in the Apostle Islands (Pycha and King 1975). As previously noted, the establishment of refuges closed to commercial and recreational harvest were an important step toward protecting and establishing spawning stocks and limiting overall fishing mortality in the surrounding area (Swanson and Swedberg 1980; Stanley et al. 1987; Hansen et al. 1995; Schram et al. 1995). Addressing incidental catch of lake trout in other

fisheries was another important component of rehabilitation efforts. For example, harvest of lake whitefish, another commercially important species, involved the use of large-mesh gill nets that also ensnared lake trout. Enhanced fishing effort for lake whitefish using this gear in the 1970s and 1980s following increases in their abundance meant that lake trout bycatch also increased during this time period (Hansen et al. 1995). Subsequent limitations to gill net lengths and size limits in the early 1990s helped to address this issue and further reduce lake trout mortality in the fishery (Hansen et al. 1995).

Additional factors that were seen as indicating progress in the resurgence of lake trout in Lake Superior included evidence of density-dependence and success of wild over stocked lake trout in driving recruitment. As noted by Bronte et al. (1995a) the existence of compensatory density-dependence in lake trout survival would indicate populations had rebounded to a maximum stock size and that rehabilitation may be complete. Such processes were not yet evident in the two decades between 1973 and 1992, and cannibalism or predation, two indications of intra-specific competition linked to density-dependence, were not considered limiting factors for the population (Bronte et al. 1995a). However, by 1995, Corradin et al. (2008) asserted that density-dependent recruitment was occurring and that cannibalism could also be playing a role in regulating population size. Several studies also noted the lesser productive success of stocked lake trout in the offshore areas of the Apostle Islands (Krueger et al. 1986; Hansen et al. 1995; Corradin et al. 2008). By the first half of the 1990s, natural reproduction and recruitment propelled by wild lake trout predominated over that of stocked fish in the Wisconsin waters of Lake Superior (Bronte et al. 1995a; Corradin et al. 2008). Subsequently, lake trout stocking ceased in 1994 in the WI-2 management unit (Seider 2010a) (Figure 2). Ultimately, the natural reproductive success of wild lake trout coupled with evidence

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of density-dependent effects defined this progress toward lake trout rehabilitation in the Apostle Islands of Lake Superior.

Lake whitefish

Lake whitefish are another ideal focal species for further evaluation of refuges in Lake Superior because of the fishery's historical status and interaction with lake trout management. Lake whitefish are a valuable commercially exploited species that has remained an important native component of Lake Superior foodwebs (Ebener et al. 2008a; Seider and Schram 2011). In addition to dominating Lake Superior's commercial fishery since the late 1980s (Bronte et al. 2003), lake whitefish also currently support the largest commercial fishery in the Apostle Islands (Seider and Schram 2011) and across the Great Lakes (Ebener et al. 2008a). As previously noted, harvest of lake whitefish with large-mesh gill nets has often also impacted lake trout due to bycatch (Hansen et al. 1995). Therefore, harvest restrictions on one species affect the other, such as limitations on the use of lake whitefish-targeted gill nets and mandatory conversions to use of trap nets (Ebener 1997; Ebener et al. 2008a). Despite the fact that the refuges were not created to enhance lake whitefish populations, lake whitefish's role as a sympatric species with lake trout (Seider and Schram 2011) means that one's management can affect the other, as demonstrated in the above example.

Similar to lake trout, lake whitefish stocks also went through dramatic declines and subsequent resurgence, with the large yields of the late 1800s declining to those of a decimated fishery by 1960 due to overfishing, habitat degradation, and invasive species impacts (Lawrie and Rahrer 1972; Ebener 1997; Ebener et al. 2008a). Subsequent fishery management actions previously mentioned, such as sea lamprey control and harvest restrictions, coupled with habitat restoration and improved water quality, helped lake whitefish stocks recover (Ebener 1997;

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Ebener et al. 2008a; Seider and Schram 2011). Increases in densities of predators, such as lake

trout, and their subsequent consumption of various invasive preyfish species (e.g., rainbow

smelt), is thought to have potentially benefitted lake whitefish by limiting the amount of

competition with, and juvenile predation from, these exotic species (Ebener et al. 2008a; Seider

and Schram 2011). These factors, coupled with strong year classes due to complimentary

environmental conditions during the late 1970s and early 1980s, facilitated the impending

recovery of lake whitefish stocks in Lake Superior (Ebener 1997).

Lake whitefish are benthivores that primarily consume amphipods, as well as insect

larvae, small clams, fish eggs, and juvenile or smaller species of fish in the Apostle Islands

region (Seider and Schram 2011). They prefer to inhabit waters in inshore habitats (Lawrie and

Rahrer 1973) at depths ranging from 18 m (and occasionally shallower) to 71 m, but they

typically remain shallower than 53 m in the Apostle Islands (Dryer 1966). They spawn in the

fall (October through December, peaking in early November) over stony bottom types, cobble,

and occasionally sand in shallow waters (under approximately five meters depth) in exposed

areas (Freeberg et al. 1990; Ebener et al. 2008a). Coberly and Horrall (1980) noted that lake

whitefish spawning often occurred in the shallower areas of reefs also used as spawning sites by

lake trout, but that the sites with the most activity were not the same as those with the highest

historical amounts of spawning lake trout. While lake whitefish spawning stock biomass is

important for productivity, actual recruitment to the population is highly variable from year to

year and is also limited by environmental and climatic conditions, such as the harshness of

winter, extent of ice cover, and spring temperatures capable of producing plankton blooms

(Taylor et al. 1987). Strong year classes seem to follow especially cold winters followed by

early mild springs, due to increased protection of eggs from wind-driven currents via ice cover

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and subsequent spring availability of zooplankton as a prey item for larval lake whitefish (Taylor et al. 1987; Freeberg et al. 1990).

Lake whitefish population dynamics are highly malleable and can quickly compensate for variations in density and the effects of external forces (Taylor et al. 1987). For example, exploitation appears to result in increased growth and reproductive rates, and earlier age of maturation (Jensen 1981; Taylor et al. 1987). Taylor et al. (1987) therefore recommended management be aimed at maintaining moderate lake whitefish spawning stocks in ways that adapt to these variations in recruitment. Additionally, actions providing a buffer against inherent recruitment variability could be beneficial (Taylor et al. 1987). It is possible, then, that that the refuges intended for protection of lake trout could be assisting in lake whitefish rehabilitation by accounting for uncertainty in lake whitefish stock assessments or population responses to harvest regulations and climatic conditions. This possibility is reiterated in a recent WDNR report by Seider and Schram (2011) regarding lake whitefish population dynamics in the Apostle Islands, which also suggested that the refuges in this area may be benefitting the local stocks.

Tagging data from the Apostle Islands reported by Dryer (1964) maintains that most lake whitefish from that region remained within approximately 8 km of tagging sites, with some straying distances above 16 km, to the longest recorded range of about 40 km. Seider and Schram (2011) assert that most other tagging studies in the Apostle Islands demonstrated that lake whitefish tagged in the area tend to remain there. I hypothesize that lake trout refuges in this region may therefore be large enough to affect lake whitefish. Such an effect could theoretically be mediated by reduced fishing mortality or indirectly through interactions with other species that have experienced refuge-related shifts in population dynamics, therefore resulting in altered levels of competition or predation.

Cisco

Cisco is the third and final focus species for this study because of its role as a native prey item of lake trout and also as an important tribal and state-licensed commercial fishery in Lake Superior. Although not endemic to the Great Lakes, these relatively long-lived, native planktivores reach maturity by ages two or three and are also commonly referred to as lake herring (Dryer and Beil 1964; Eshenroder and Burnham-Curtis 1999). As pelagic fish, ciscoes are most commonly found at depths ranging 18 – 53 meters in the Apostle Islands (Dryer 1966). Habitat preference by ciscoes appears to shift according to life stage and according to size-class across nearshore and offshore areas (Stockwell et al. 2006). They also undergo diel migrations which appear to be mediated according to a combination of prey availability (Eshenroder and Burnham-Curtis 1999) as well as predation risk linked to light levels (Hrabik et al. 2006; Jensen et al. 2006). During the spawning season which peaks at the end of November through the beginning of December, ciscoes can be found in depths ranging from five to 128 m (Dryer and Beil 1964) but are rarely in depths beyond 73 m (Coberly and Horrall 1980). They congregate at inshore benthic zones prior to migrating higher in the water column, or even to the surface, to spawn without demonstrating any particular preference for substrate type (Dryer and Beil 1964; Selgeby 1982), which can impact their catchability with different gears. These shifts according to life stage and activity therefore also affect how cisco are targeted by fishermen, such as when gravid females that are predominantly pelagic during the spawning season are targeted for roe (egg) collection purposes (Yule et al. 2006). This focus can have implications for fishing activity in the refuges where special use zones were specifically created for access to cisco harvest.

According to Dryer and Beil (1964), cisco supported the most productive fishery in the Great Lakes from the early 1900s onward, even after historic collapses in Lake Erie by 1925.

The fishery largely targeted spawning aggregations (Stockwell et al. 2009), and its economic importance in Lake Superior was even more prominent after the collapse of the commercial lake trout fishery in Wisconsin waters (Selgeby 1982). However, cisco stocks also collapsed by the early 1960s in the Apostle Islands region and decades earlier in other areas of the lake (Selgeby 1982). This collapse was primarily attributed to excessive exploitation (Selgeby 1982). Others also assert that the decline of cisco populations in the 1950s and 1960s was exacerbated by lack of strong recruitment events (possibly caused by unfavorable environmental conditions in the twenty years prior to collapse), as well as competition with exotic rainbow smelt (Stockwell et al. 2009).

Although evidence of population recovery exists in Lake Superior (Stockwell et al. 2009), rehabilitation continues to be sporadic, and cisco still have not mirrored the success stories of lake trout or lake whitefish rehabilitation. This may be due to high variability in year-class strength typically exhibited by this species due to density-independent environmental factors (Bronte et al. 2003), as well as fluctuations in adult sex ratios and delayed female age-at-maturity driven by changing population densities (Bowen et al. 1991; Stockwell et al. 2009). Predation from, and competition with, exotic rainbow smelt may have continued to play a role in recent cisco population trends (Cox and Kitchell 2004; Myers et al. 2009). Declines in rainbow smelt following predation from lake trout could have improved cisco recruitment success since the 1980s and could prove promising for the future (Cox and Kitchell 2004; Gorman 2007). How this dynamic will balance with increasing incidence of coregonids in lake trout diets since this fish community shift (Ray et al. 2007) remains to be seen. This cautionary point also noted by Cox and Kitchell (2004) may be playing out, given that the last couple years have shown another decline in relative cisco biomass in Lake Superior (Gorman et al. 2010).

Goals and objectives

The goal of this study was to evaluate the potential effects of lake trout refuges in the Apostle Islands region of Lake Superior on three select native species of the local fish community. Beyond assessing whether these protected areas are continuing to benefit their intended focal species, I aimed to further understand if the refuges served a purpose for other commercially relevant and ecologically important species.

The objectives of this project were therefore to: 1) analyze trends in relative abundance of lake trout within and outside of the refuges to corroborate past refuge-linked evidence of rehabilitation, and 2) determine whether there is evidence that these refuges may be directly or indirectly effecting trends in relative population abundance of non-target species (i.e., lake whitefish and lake herring) in this area.

METHODS

Study site

This study focuses on the waters in the Apostle Islands region of Lake Superior, the northernmost and largest of the Great Lakes. Located along the southwestern coast of the lake within waters under the jurisdiction of the state of Wisconsin, the 22 islands making up this archipelago are contained within the WI-2 management unit (Figure 2) which has a surface area of 4,473 square kilometers (Seider and Schram 2011). The area is characterized by numerous underwater rocky reefs and shoals, complex shorelines, and a large variety of depth strata that provide an abundance of fish habitats (Coberly and Horrall 1980; Johnson et al. 2004; Seider and Schram 2011). The majority of the waters in this area are less than 80 meters deep, with a trench along the eastern portion reaching depths of 140 m (Seider and Schram 2011). The main reason

for choosing the WI-2 management area as the study site is because of its inclusion of two lake trout refuges (Figure 1).

As previously noted, these refuges were created to enhance lake trout rehabilitation efforts in Lake Superior (Stanley et al. 1987; Hansen et al. 1995). The resulting Gull Island Shoal Refuge and Devils Island Shoal Refuge were named after reefs contained within the area which were known to be historically important lake trout spawning sites (Coberly and Horrall 1980). Both refuges' principal conservation focus is "Sustainable Production," and so they are meant to support continued exploitation of biotic natural resources, such as fish, that may depend on the protected area for sensitive life stages (NOAA 2011a). Included in the area is Gull Island reef, which is approximately 16 km long and ranges from 1.6 to 4.8 km wide, is surrounded by deep water channels, and is linked to Michigan Island, Gull Island, and Gull Island Shoal, which projects upward to about 5.5 meters below the water's surface (Swanson and Swedberg 1980). A lake trout nursery area exists near Michigan Island (Bronte et al. 1995b; Schram et al. 1995). The Gull Island Shoal Refuge was established around and beyond this shoal and reef complex in 1976 and served to primarily protect remnant spawning stocks of lake trout (Swanson and Swedberg 1980; Stanley et al. 1987; Hansen et al. 1995; Schram et al. 1995). The lack of previously existing geo-referenced digital maps of the refuge boundaries necessitated that I create such maps according to the state's annual fishing regulations (WDNR 2011) and the Wisconsin Administrative Code (Wis. Admin. Code NR 26.23, Oct. 2010) to depict their spatial extent and relative location of sampling sites used in data collections for fish community assessments by the Wisconsin Department of Natural Resources (WDNR). For a description of the methods used to accomplish this digitization, please refer to the Appendix. Once georeferenced, I then analyzed the resulting refuge polygon in ArcGIS version 10 (ESRI 2011), and calculated that the refuge encompasses a maximum area of approximately 724 km^2 if

defined according to the maps pictured in the state fishing regulations, and approximately 447

km^2 if defined according to the State Administrative Code, which allows for licensed

commercial fishing in areas of the refuge where depths exceed 64 m, as identified in Figure 3.

In addition to the first refuge, the WDNR also established the Devils Island Shoal Refuge in

1981 to complement stocking efforts toward re-establishing a naturally reproducing stock at this

historic spawning location (Coberly and Horrall 1980; Stanley et al. 1987; Hansen et al. 1995;

Bronte et al. 2002). I determined the approximate maximum area of this refuge (not including

open fishing zones during certain seasons) to be 478 km^2. Together (not including the

commercial fishing zone within the Gull Island Shoal Refuge), the two refuges cover

approximately 21% of the total area in the WI-2 management unit.

When the refuges were established, the primary intent was to supplement lake trout

rehabilitation efforts through prohibition of commercial and recreational fishing for all species in

these areas. However, over the past several decades since establishment, some areas have been

exposed to various levels of fishing mortality. For instance, within the Gull Island Shoal Refuge,

in addition to the commercial fishing zone (pictured in Figure 3), a cisco fishery is zoned from

November through mid-December where bottom depths are less than 45.7 m, and a month-long

Menominee whitefish (*Prosopium cylindraceum*) fishery exists during the fall in waters

adjoining Michigan Island out to maximum bottom depth of 12.8 m (Wis. Admin. Code NR

26.23, Oct. 2010). Additionally, a relatively small section at the southwest corner of Devils

Island Shoal Refuge (see Figure 3) is also open to recreational and commercial fishing during the

summer months, from June 1 through September 30 (Wis. Admin. Code NR 26.23, Oct. 2010).

The extents of these zones are further depicted in the Appendix, in Figure 16. There are also a

number of limited special use zones for tribal fisheries targeting specific species at certain times
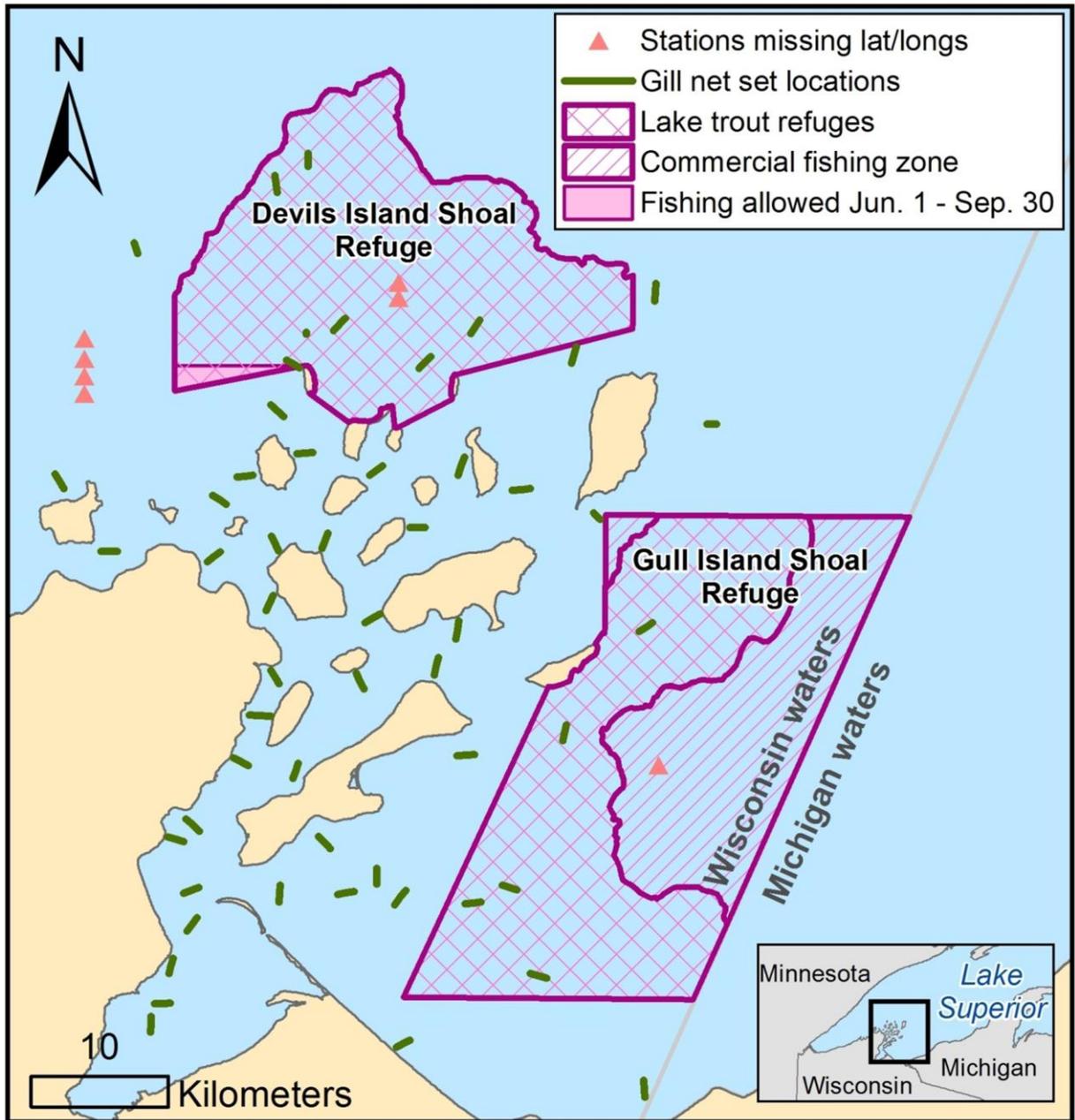
FIGURE 3. Lake trout refuges and graded-mesh gill net stations sampled in even years by the Wisconsin Department of Natural Resources (WDNR) from 1982 – 2010 in the Apostle Islands area. (Inset: Western Lake Superior). Full refuge extent is indicated by the purple line surrounding cross-hatching. Licensed commercial fishing is allowed in the zone indicated by diagonal simple-hatch; licensed fishing of all forms is allowed during the summer months in the zone indicated in solid pink. Stations missing coordinates but identified by the WDNR as being located inside or outside of the refuges are indicated by orange triangles and are not representative of exact locations. Refer to the Appendix for more information about the boundaries of additional fishing zones, description of mapping methods, and complete list of base layer data sources.

based on state-tribal agreements that are renegotiated every ten years (Seider and Schram 2011; WDNR et al. 2005). In addition to the above exceptions, the current co-management agreement in effect since 2005 includes open zones for take of ciscoes within the southwestern corner of the Devils Island Shoal Refuge for two months during the winter (November 15 through January 15) and the use of non-mechanical gill nets up to lengths of 800 ft. (244 m) in a specific area of the refuge during the summer months (June 1 through September 30) with mandatory observation of catch-per-unit-effort. However, for the analysis, I assumed the effects of these fisheries were negligible on the larger trends in relative abundance observed in lake trout and lake whitefish during assessment surveys.

Data collection

Several agencies and organizations in the general vicinity of the study region conduct fisheries-related monitoring and research. In addition to various academic research institutions, these include the United States Geological Survey, the U.S. Fish and Wildlife Service, the WDNR, the Michigan Department of Natural Resources (MDNR), the U.S. National Park Service, the Red Cliff Band and the Bad River Band of the Lake Superior Tribe of Chippewa Indians, the Great Lakes Indian Fish and Wildlife Commission, and the Chippewa Ottawa Resource Authority. After a survey of available datasets, I chose to base my analysis on data collected by the WDNR's Bayfield Office for several reasons. First, the WDNR possessed a long-term, fishery-independent dataset collected from an extensive number of sites spanning areas both within and outside of the refuges in the study area. Second, as described further below, these data were collected as part of a consistent monitoring program for multiple species of the local fish community, therefore reducing variability in effort and biases, such as different gear specifications affecting catchability rates.

The purpose of this graded-mesh gill net survey, also referred to as the summer index assessment, was to "monitor various population dynamics (e.g. abundance, population structure) of the Lake Superior fisheries and to record potential shifts in the fish community structure" (Seider 2010b). The use of differently sized mesh panels (with mesh sizes ranging from 38.1 mm to 177.8 mm in 12.7 mm increments) meant that a variety of different sizes and species of fish could be representatively sampled with this gear. In particular, I was able to obtain relative abundance data for the three species of interest in this study (lake trout, lake whitefish, and cisco) collected annually with one gear type, at the same stations during the same time of year. While both lean and siscowet lake trout inhabit the study area (Bronte et al. 2003), the data I analyzed only included lean lake trout, so I did not evaluate different morphotypes as part of this analysis. According to a study completed by Dryer (1966), the three species I focused on were historically among those most commonly captured in the same depth strata in the Apostle Islands (18 − 53 m), and as such, effectively gave me a comparative assessment of changes in the relative abundance of these components of the fish community.

The sites sampled as part of this survey were monitored with gill nets of the same length (3,600 ft., or about 1 km, of monofilament gill net) that were each set for one night (spanning a 24 hour period) at each station (Seider 2010b). This consistent effort corresponding to catch enabled me to work directly with count data during subsequent data analysis, as the constant effort meant that counts were, in effect, standardized to catch-per-unit-effort (CPUE).

Data provided to me by the WDNR included measurements collected at a total of 66 stations during surveys conducted from 1970 through 2010. These standardized summer index sites were located to follow temporal trends in relative abundance of members of the fish community (Michael Seider, U.S. Fish and Wildlife Service (formerly of WDNR), personal communication). As WDNR index stations, I assumed these sites positioned throughout WI-2

satisfied assumptions for a random sampling design, based off of the Lake Superior Technical Committee's treatment of data from the spring index surveys as a simple random sample (Ebener 2003). However, all stations were not consistently sampled every year of the time series, because different stations were added, dropped, or only sampled in even or odd years. This resulted in missing data for certain stations in certain years. After discussions with WDNR biologists, I decided not to discard data from discontinued stations, because they were not removed from the survey for reasons likely to bias results (such as discontinuation of stations with low fish yields). Data from all these sites were used by the WDNR in calculating average annual CPUE for the Wisconsin waters of Lake Superior (Seider 2010b; Michael Seider, personal communication), so I also used them for evaluation of long term patterns in the data for the WI-2 management unit as a whole. However, only a small proportion of sites were sampled during odd years after 1980, and none of those sampled in odd years included stations located inside either of the lake trout refuges. Additionally, only three stations inside the refuges were monitored prior to 1980. Therefore, I limited my analysis of refuge effects to only data collected after 1981 (the time after which both refuges had been implemented, since data prior to that was so limited) and during even years (because that was the only time the refuges were sampled) to ensure the data consistently represented areas within and outside of the refuges.

The ultimate subset of the WDNR dataset I used for the refuge analysis included data from 14 even years spanning 1982 through 2010 (data were not available from 1996) and a total of 61 stations. Of these stations, 14 were located inside the refuges (eight in Devils Island Shoal Refuge and six in Gull Island Shoal Refuge) and 47 were located outside refuge boundaries (see Figure 3). Some stations were discontinued at certain points, meaning these stations were only sampled for a portion of the total time span but still had sufficient data to determine a trend (22 stations were sampled for two to nine years, and one station had 13 years of data). The

remaining 38 stations were sampled each of the 14 years used for this analysis. The WDNR

shifted from the use of multi- to monofilament nylon nets in 1991, but I did not explicitly

incorporate the potential effects of this change on catchability in my analyses, as the gear

improvement was applied concurrently to all sampling stations. As such, I assumed this factor

would not impact my overall comparisons of relative abundances of fishes between stations

within and outside the refuges.

The WDNR dataset identified which stations were located within each of the refuges. To

confirm these distinctions, I also mapped the location of each station in ArcGIS (ESRI 2011) and

verified whether they fell within or outside of the geo-referenced refuge boundaries. As

identified in Figure 3, some stations were missing latitude and longitude information because

their monitoring was discontinued before this type of spatial information was regularly recorded

in a format I could map with a sufficient level of accuracy. However, because the WDNR

identified these seven stations as being outside or inside the refuges (and specified which one), I

felt sufficiently confident in their relative locations, despite the coarser resolution, for use of their

data in the analysis.

Analytical approach

Marine reserve evaluations are frequently based on measurement of changes in metrics

that include fish density or biomass, size, and species diversity (Nowlis and Friedlander 2004).

These are often analyzed with a control-impact design, in which the metric of interest is

compared inside the reserve versus outside, or the ratio of the value of the metric inside the

refuge over the value outside is evaluated over a series of measurements (Russ and Alcala 1996;

Willis et al. 2003a; Micheli et al. 2004). Since determination of fish density using data collected

solely from gill nets is difficult owing to the lack of an accurate measurement of water column

volume or bottom area sampled, I chose to use relative fish abundance (average annual count per unit of effort) as my metric of interest. Additionally, the area sampled per site did not vary substantially during the study because net lengths did not change, so relative abundance was considered a comparable metric to density for use in evaluation of the refuges. I compared annual means for this metric from inside the refuges to those measured outside the refuges over the time period using a general linear model to test for differences in trends in each area. The fact that I was averaging data collected from two reserves allowed for replication at the reserve level, which potentially limited bias associated with the individual areas (Willis et al. 2003a).

While it would have been preferable to have had sufficient data from before refuge implementation to compare with data after refuge establishment in order to implement a before-after-control-impact design (Stewart-Oaten et al. 1992; Stewart-Oaten and Bence 2001; Gotelli and Ellison 2004), I had a sufficiently long time series that allowed me to compare trends after protection. This approach is considered to be an adequate method for monitoring refuge effects (Nowlis and Friedlander 2004) and has been demonstrated in evaluations of reserves in the marine environment (e.g., Russ and Alcala 1996, 2003).

I began by conducting an exploratory analysis of the data. I first evaluated histograms of the count data to visually assess their distribution. I repeated this for each species' entire dataset, as well as for the data separated according to catch sampled from stations inside and outside of the refuges. I also visually compared box plots of the number of fish caught from stations inside the refuges versus outside to note if apparent differences existed. To visually evaluate general changes in the raw count data over time before and after refuge implementation, I calculated the mean annual catch collected from all sampling stations by the WDNR (66) from 1970 – 2010. I plotted these means against time for catches of lake trout, lake whitefish, and cisco. Next, using only the subset of the data chosen for the refuge effects analysis (as described in the above

section for *Data Collection*), I calculated the mean annual log-transformed catch of each species

sampled at stations inside the refuges and again for stations outside the refuges, and I plotted this

against time, in even years, beginning in 1982 through to 2010. Given the past analyses showing

that wild lake trout were more successful than stocked lake trout for driving recruitment in the

study area (Krueger et al. 1986; Hansen et al. 1995; Corradin et al. 2008), I also prepared these

plots for wild lake trout (identified in the dataset as having no fin clip) and stocked lake trout

(identified through existence of a fin clip). I used the open source R software (hereafter referred

to as R) provided by the R Development Core Team (2011) for the preparation of all analytical

graphs and statistical analyses performed in this study, unless otherwise noted.

To test significance of patterns visualized in the data, I performed multiple linear

regressions on the study species' count data using an explanatory model I developed to account

for refuge effects over time. My model used in these analyses of trends in relative species

abundance was based on the exponential population growth model (Quinn and Deriso 1999)

(equation 1):

$$N_t = N_0 * e^{(r*t)} \qquad (1)$$

Where N_t is the population at a given point in time, N_0 is initial population size, r is the

instantaneous growth parameter, and t is time. I then expanded the model to include a factor

variable for refuge status (in versus out) and its effects over time. Incorporating these terms into

the population growth model provided me with the following theoretical model (equation 2):

$$N_t = N_0 * e \wedge [(r*t) + (b_2 * R) + (b_3 * R * t) + \varepsilon] \qquad (2)$$

In this equation, relative abundance (N_t) is equivalent to catch-per-unit-effort (CPUE) as the

response variable, R represents an indicator variable for refuge status, t represents the continuous

variable, time in years, and ε represents the error associated with the model. The independent

variables were treated as fixed effects. The use of a fixed effects model for evaluating reserves

has also been demonstrated by Willis et al. (2003a).

I next took the natural logarithm of the exponential theoretical model (equation 2) to

linearize it (Gotelli and Ellison 2004) to the form shown in equation (3). Therefore, I also

succeeded in reducing the exponential equation into a general multiple linear regression model

(equation3):

$$\log_e(CPUE) = \beta_0 + (\beta_1*t) + (\beta_2*R) + (\beta_3*R*t) + \varepsilon \qquad (3)$$

Where β_0 is the logarithm of the initial population size (N_0), β_1 is the instantaneous population

growth rate, β_2 is the magnitude of the refuge main effect, and β_3 is the strength of the

interaction term. In order to accommodate the log-transformation of a dependent variable that

included zero values, I applied an additive constant of 0.5 to all catch data before the

transformation (Yamamura 1999), because it is half of the smallest observed discrete non-zero

catch value (one). I chose this value to reduce the amount of bias that could result from using a

larger arbitrary value, such as 1.0 (Yamamura 1999). The existence of both categorical and

continuous variables within the equation (3) meant the multiple linear regression was, in fact, an

analysis of covariance (ANCOVA) (Gotelli and Ellison 2004). I included a term for the

interaction of time and refuge status in the model, because it allowed me to test whether the slope

of trends in CPUE depended on refuge status. In other words, the interaction term refers to the

magnitude of increase in the rate of growth over time for CPUE from within the refuges versus

CPUE from external areas without such limitations to fishing mortality. This model was meant

to be explanatory, as opposed to predictive, and so my intention was not to estimate parameter

values for use in modeling future predictions of population size. My primary interest was

whether the model identified if the variables of time and refuge status affected the relative

abundance of each species, and in which direction. In this model, CPUE is equivalent to total counts of fish sampled per gill net lift (number caught per single net per night). Effort was the same across all samples, because only one gill net of the same length and type was set for a single net-night at each station surveyed in a particular year. Therefore, I was able to use the raw counts of fish from each net without needing to correct for effort. Since this effort also remained constant throughout the study dataset, CPUE is also simply referred to as catch or relative abundance in other portions of the analysis.

As previously mentioned, assessing the potential difference in the slope of the population abundances over time between factors (inside the refuges versus outside) was the primary focus for this analysis. Evaluating differences between trends of continuous variables according to a categorical factor is an accepted methodological approach (Kutner et al. 2005) and has been implemented by others in ecological analyses (Alcalá and Domínguez 2005). This approach has also been applied to modeling of fisheries data to evaluate changes in catch over time in different areas where fishing occurs (Maunder and Punt 2004), with significant interaction terms indicating that the slope of the temporal trend in catch varied with location (Hilborn and Walters 1992).

I performed the ANCOVA with the "lm" function in the "stats" package for R (R Development Core Team 2011). I identified whether the model terms were significant ($P \leq$ 0.05), indicating that their hypothesized effects on the patterns exhibited in the dependent variable were unlikely due to pure random chance. I also evaluated the significance of the model's F-test statistic to determine the overall fit of the model and the R^2 value to identify the amount of variation explained by the model. To visualize the model results, I plotted predicted values over the calculated annual log-transformed means of relative abundance. This analysis was repeated for each species' count data, as well as for wild and stocked lake trout.

To verify whether modeled results met assumptions of normality, equal variance, and independence of errors, I examined each model's residuals with a variety of graphical approaches. I began by constructing a histogram of the residuals to assess whether they appeared to follow a normal distribution. Next, I examined a series of regression diagnostic plots created by the "plot.lm" function in the R stats package (R Development Core Team 2011). I focused specifically on residuals plotted against fitted values to assess homogeneity of variance, and the normal quantile-quantile plots of the standardized residuals against theoretical quantiles from a normal distribution to assess normality of errors. The closer the data points were to a line defining a 1:1 ratio between the residual quantiles and the normal quantiles, the more likely the regression satisfied the assumption of having an error structure following a normal distribution (Maindonald and Braun 2007). To specifically evaluate whether errors were independent, I visually inspected plots of model residuals against time and plots of autocorrelation estimates against time lags using the "acf" function in the R "stats" package (R Development Core Team 2011). I also performed a Durbin-Watson test for autocorrelation with the "dwt" function in the "car" package (Fox and Weisberg 2011) for R (R Development Core Team 2011).

RESULTS

Annual mean catch of lake trout collected during the graded-mesh gill net survey since the 1970s did not increase overall ($F = 1.935$; df $= 1, 980$; $P = 0.165$). However, as shown in Figure 4, there were spikes in lake trout counts during the immediate years following establishment of the refuges, and a slight upward trend existed from this point until the early 2000s. This increase did not continue through to 2010, as a period of declines in annual mean catch became apparent in more recent years. In fact, a linear regression of all the count data
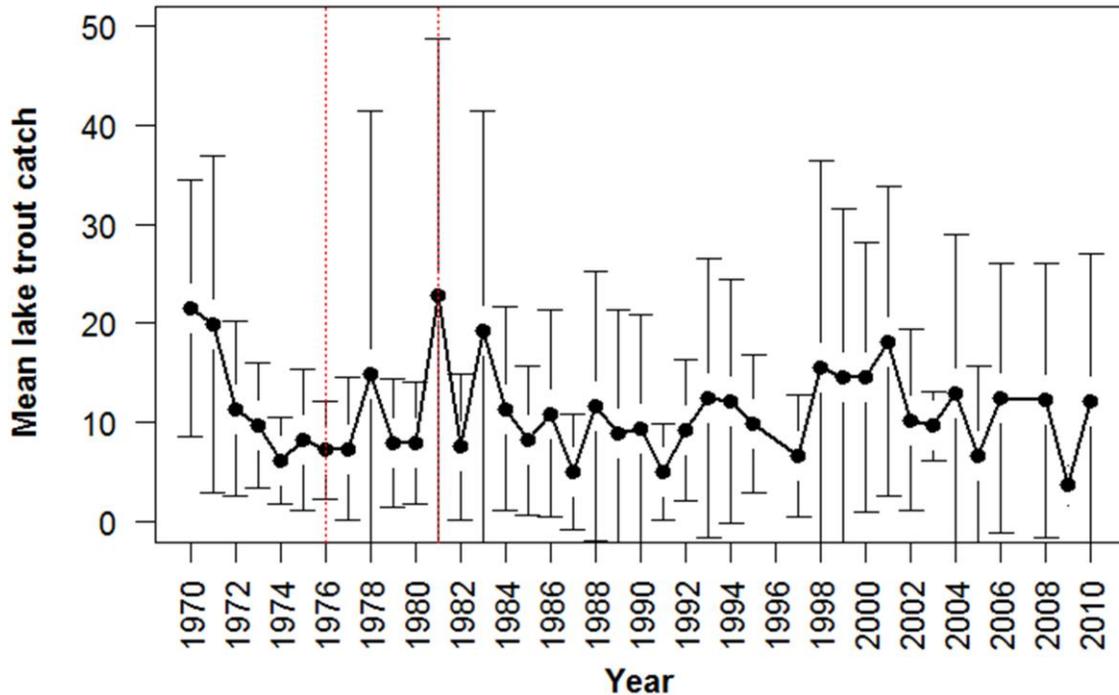
FIGURE 4. Annual mean lake trout (*Salvelinus namaycush*) catch (+/- SD) from 1970 through 2010. The red dotted vertical lines correspond to establishment of the Gull Island Shoal Refuge (1976) and the Devils Island Shoal Refuge (1981). Data are included from all stations sampled by the Wisconsin Department of Natural Resources in the WI-2 management unit during the annual summer graded-mesh gill net survey. Data were not available for 1996 and 2007.

(without refuge status specification) solely against time as the independent variable for catch

data collected after both refuges' establishment (1982 onward) did not show a significant trend

($F = 1.582$; df = 1, 755; $P = 0.209$). Similarly, a linear regression of the data used in the refuge

analysis (data from even years during the period of 1982 – 2010) did not show a significant trend

either ($F = 1.349$; df = 1, 691; $P = 0.246$).

However, when the data were analyzed with the interaction of refuge status and time

incorporated in the model (refer to equation 3), results indicated the slopes of trends in lake trout

relative abundance were significantly different depending on whether they corresponded to the

area inside or outside of the refuges. This conclusion is based on the existence of a significant

interaction term (0.026; see Table 1). In other words, the year effect is dependent on refuge

status (in or out). The positive value of this term signifies that for every unit increase in time, the log-transformed average lake trout catch from inside the refuges increased relative to the area outside of the refuges. This divergence of trends in relative abundance according to refuge status is visible in Figure 5. In addition, the trend lines corresponding to the predicted values in catch (Figure 5) demonstrate that relative abundance was higher within the refuges overall, which is supported by the significance of the refuge term in the model (Table 1). Finally, although the ANCOVA demonstrated a significant overall model fit ($F = 36$; df = 3, 689; $P = < 2.2E\text{-}16$), interpretation of the adjusted R^2 value shows the model only explained a low percentage (13.18%) of the total variability in the dependent variable. This result emphasizes the fact that the heterogeneity in lake trout count data is likely influenced by other factors, beyond just the variables of time and refuge status, such as natural mortality, intraspecific competition, and species interactions, among others.

Separate analyses of wild and stocked lake trout demonstrated an even stronger indication of a refuge effect in only wild fish. As shown in Figure 6, while the initial relative abundances of stocked lake trout in the early 1980s were greater than those for wild lake trout (respective to areas within and outside of refuges), wild lake trout quickly increased inside the refuges and dominated from 1986 onward. After 1996 (once stocking had ceased in the region in 1994) stocked lake trout declined, as expected, to relative abundances below those of wild lake trout inside and outside of the refuges (Figure 6). Results of the model fit for relative abundances of wild lake trout ($F = 89.32$; df = 3, 689; $P = < 2.2E\text{-}16$) showed a higher adjusted R^2 (0.2769) than when I performed the original ANCOVA on all lake trout counts without hatchery origin-fish removed from the dataset. This result indicates that the model accounted for a larger portion of the variability in wild fish abundance than for lake trout from all origins (both naturally

TABLE 1. Lake trout (*Salvelinus namaycush*) linear model terms and associated ANCOVA parameter estimates. "Refuge status" corresponds to the treatment (inside refuge boundaries) and control (outside refuge boundaries) areas. Asterisks denote level of significance ($P \leq 0.05*$).

Model Term	Estimate	Standard error	P-value	
(Intercept)	3.627	9.588	0.7054	
Year	-8.973E-04	4.807E-03	0.8520	
Refuge status	-50.970	20.270	0.0121	*
Year × Refuge status	0.026	0.010	0.0107	*
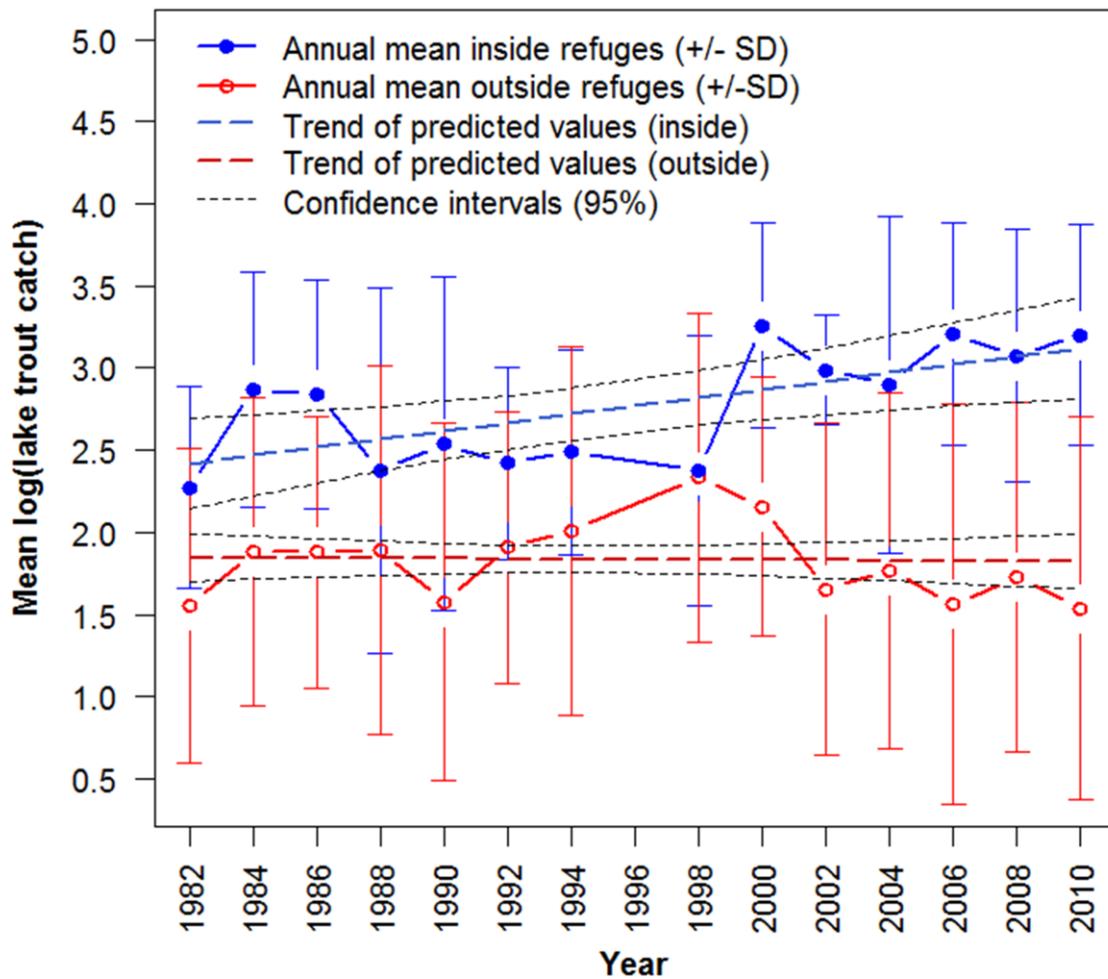
FIGURE 5. Annual log-transformed mean lake trout (*Salvelinus namaycush*) catch against time, inside (blue with closed circles) vs. outside (red with open circles) of the refuges. The blue and red dashed lines are the predicted values of the model fitted with the parameter estimates in Table 1, and correspond to inside and outside of the refuges, respectively. Error bars are +/- one standard deviation (SD) from the annual means; the fine dotted black lines correspond to the 95% confidence intervals of the predicted values.
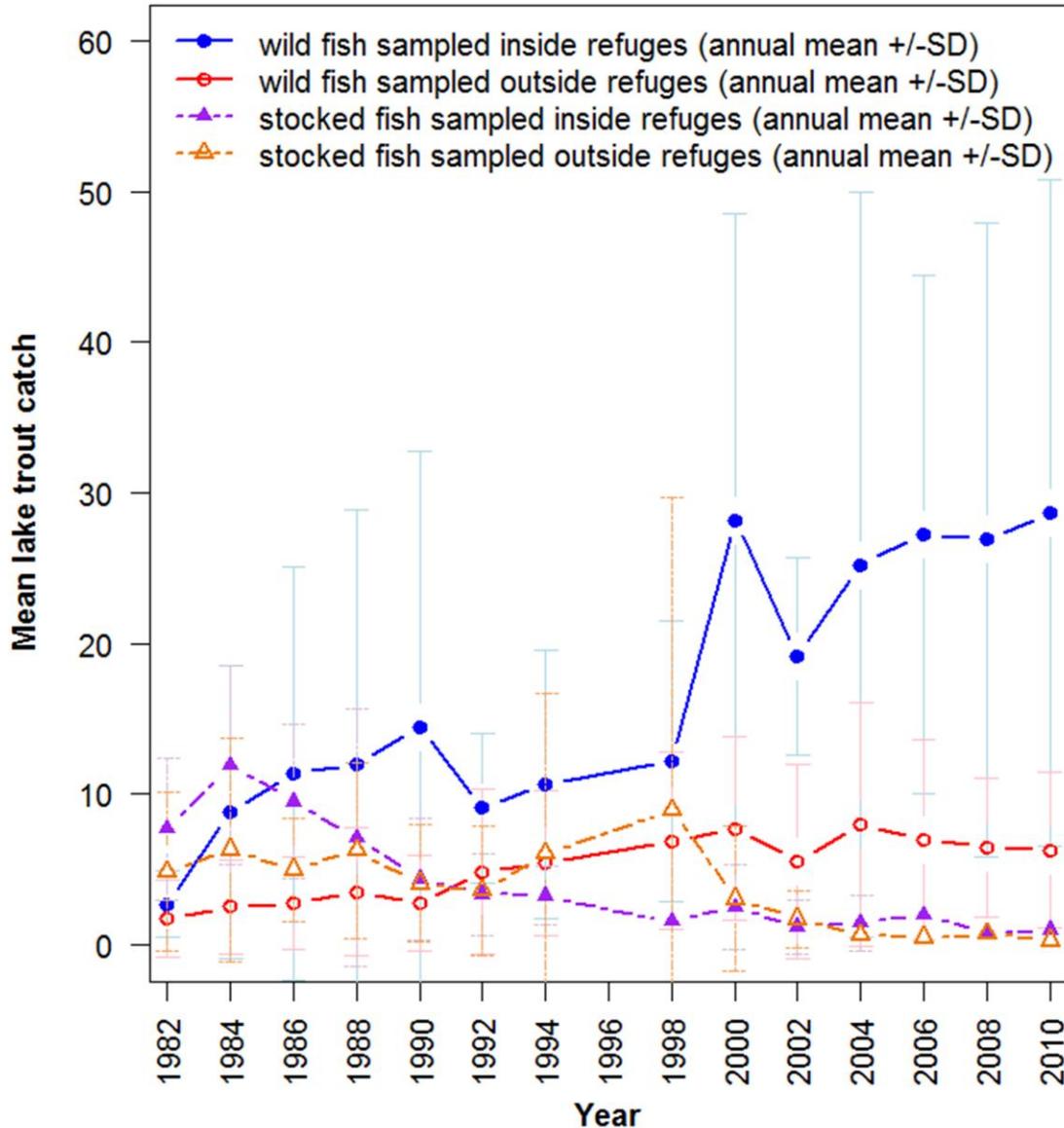
FIGURE 6. Annual mean catches of wild and stocked lake trout (*Salvelinus namaycush*) against time, inside vs. outside of the refuges. Error bars are +/- one standard deviation (SD) from the annual means.

produced and hatchery-reared). Although this analysis showed increasing trends for wild fish

both inside and outside of the refuges (Figure 7), the significant model interaction term (Table 2)

indicated that wild like trout increased at a greater rate inside the refuges than outside on a

logarithmic scale. The decreasing trend in stocked lake trout is further demonstrated in Figure 8.
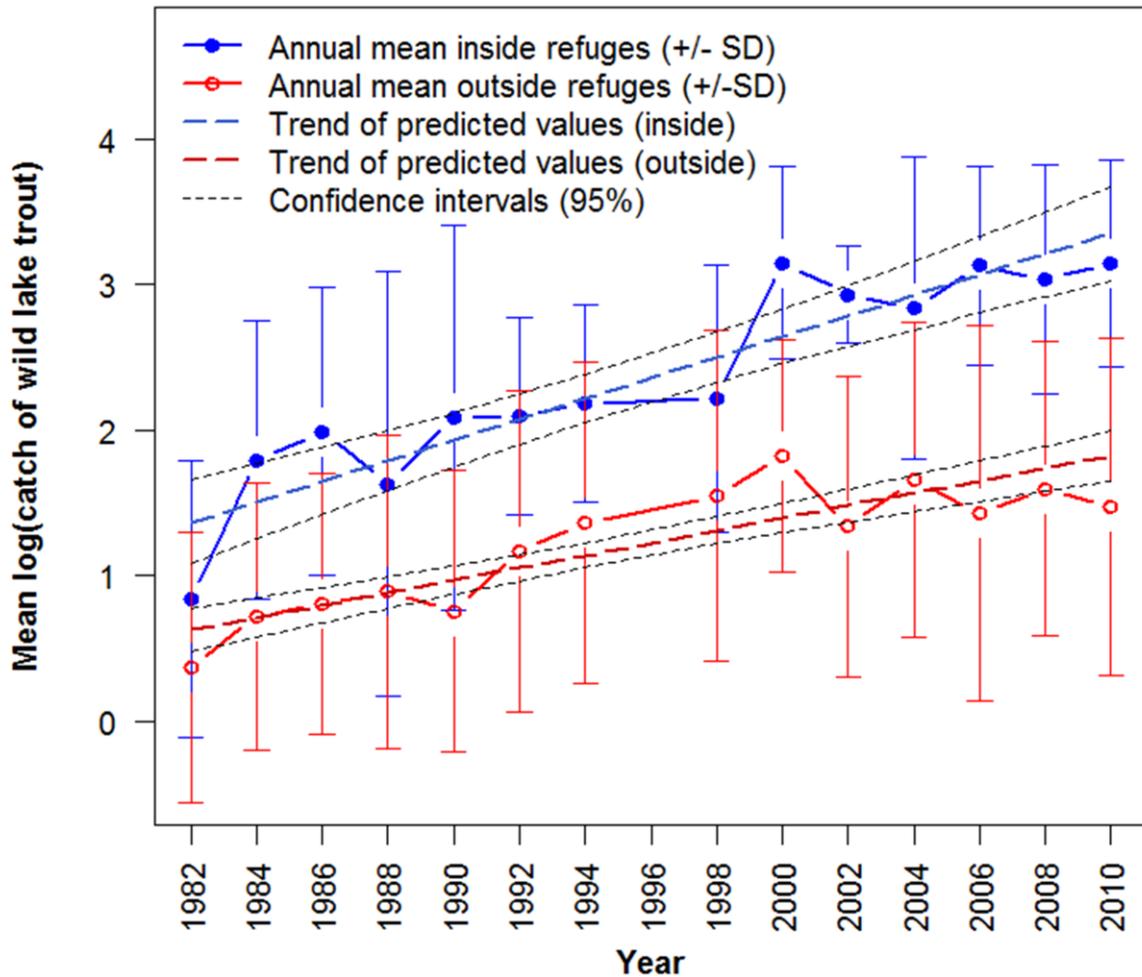
FIGURE 7. Annual log-transformed mean wild lake trout (*Salvelinus namaycush*) catch against time, inside (blue with closed circles) vs. outside (red with open circles) of the refuges. The blue and red dashed lines are the predicted values of the model fitted with the parameter estimates in Table 2, and correspond to inside and outside of the refuges, respectively. Error bars are +/- one standard deviation (SD) from the annual means; the fine dotted black lines correspond to the 95% confidence intervals of the predicted values.

TABLE 2. Wild lake trout (*Salvelinus namaycush*) linear model terms and associated ANCOVA parameter estimates. "Refuge status" corresponds to the treatment (inside refuge boundaries) and control (outside refuge boundaries) areas. Asterisks denote level of significance ($P \leq 0.01**$, $P \leq 0.001***$).

Model Term	Estimate	Standard error	P-value	
(Intercept)	-83.896	10.004	2.83E-16	***
Year	0.043	0.005	< 2E-16	***
Refuge status	-54.946	21.147	0.0096	**
Year × Refuge status	0.028	0.011	0.0082	**

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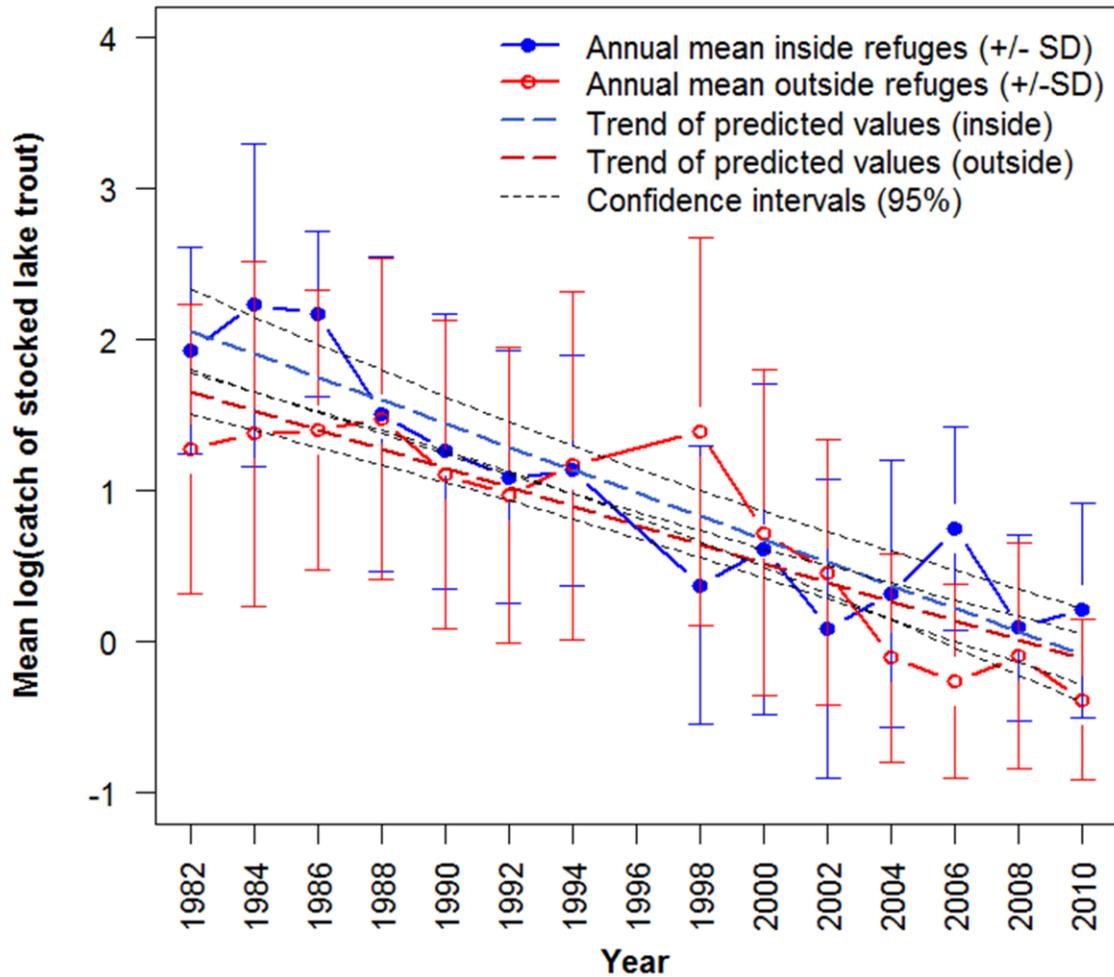
FIGURE 8. Annual log-transformed mean stocked lake trout (*Salvelinus namaycush*) catch against time, inside (blue with closed circles) vs. outside (red with open circles) of the refuges. The blue and red dashed lines are the predicted values of the model fitted with the parameter estimates in Table 3, and correspond to inside and outside of the refuges, respectively. Error bars are +/- one standard deviation (SD) from the annual means; the fine dotted black lines correspond to the 95% confidence intervals of the predicted values.

Evaluation of the model results (ANCOVA: $F = 81.66$; df = 3, 689; $P = < 2.2E\text{-}16$) showed that the stocked lake trout model accounted for 25.9% of the variability according to the adjusted R^2 value, but the lack of a significant interaction term meant that I could not reject the null hypothesis that there was no difference between the trends in relative abundance of stocked fish inside versus outside of the refuge (Table 3). However, when I dropped the interaction term

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from the model, significant main effects did exist for both year and refuge status (Table 4). This was not necessarily consistent with a refuge effect, because the slightly higher abundance inside the refuges could be due to other factors, such as stocking location. These findings however, supported the conclusion that wild lake trout continue to play a more prominent role in supporting increased abundances than stocked lake trout, and this trend appears to have increased within refuge boundaries.

TABLE 3. Stocked lake trout (*Salvelinus namaycush*) linear model terms and associated ANCOVA parameter estimates. "Refuge status" corresponds to the treatment (inside refuge boundaries) and control (outside refuge boundaries) areas. Asterisks denote level of significance ($P \leq 0.001$***).

Model Term	Estimate	Standard error	P-value	
(Intercept)	126.353	9.686	<2E-16	***
Year	-0.063	0.005	<2E-16	***
Refuge status	27.154	20.475	0.185	
Year × Refuge status	-0.013	0.010	0.189	

TABLE 4. Stocked lake trout (*Salvelinus namaycush*) linear model terms (with non-significant interaction term dropped to allow for interpretation of main effects) and associated ANCOVA parameter estimates. "Refuge status" corresponds to the treatment (inside refuge boundaries) and control (outside refuge boundaries) areas. Asterisks denote level of significance ($P \leq 0.05$*, $P \leq 0.001$***).

Model Term	Estimate	Standard error	P-value	
(Intercept)	132.379	8.538	<2E-16	***
Year	-0.066	0.004	<2E-16	***
Refuge status	0.229	0.091	0.012	*

The annual means of lake whitefish counts collected in the WI-2 management unit during the graded-mesh gill net survey since the 1970s exhibited a marked increase beginning in the years following establishment of the second refuge (Figure 9). Upon initial inspection of the
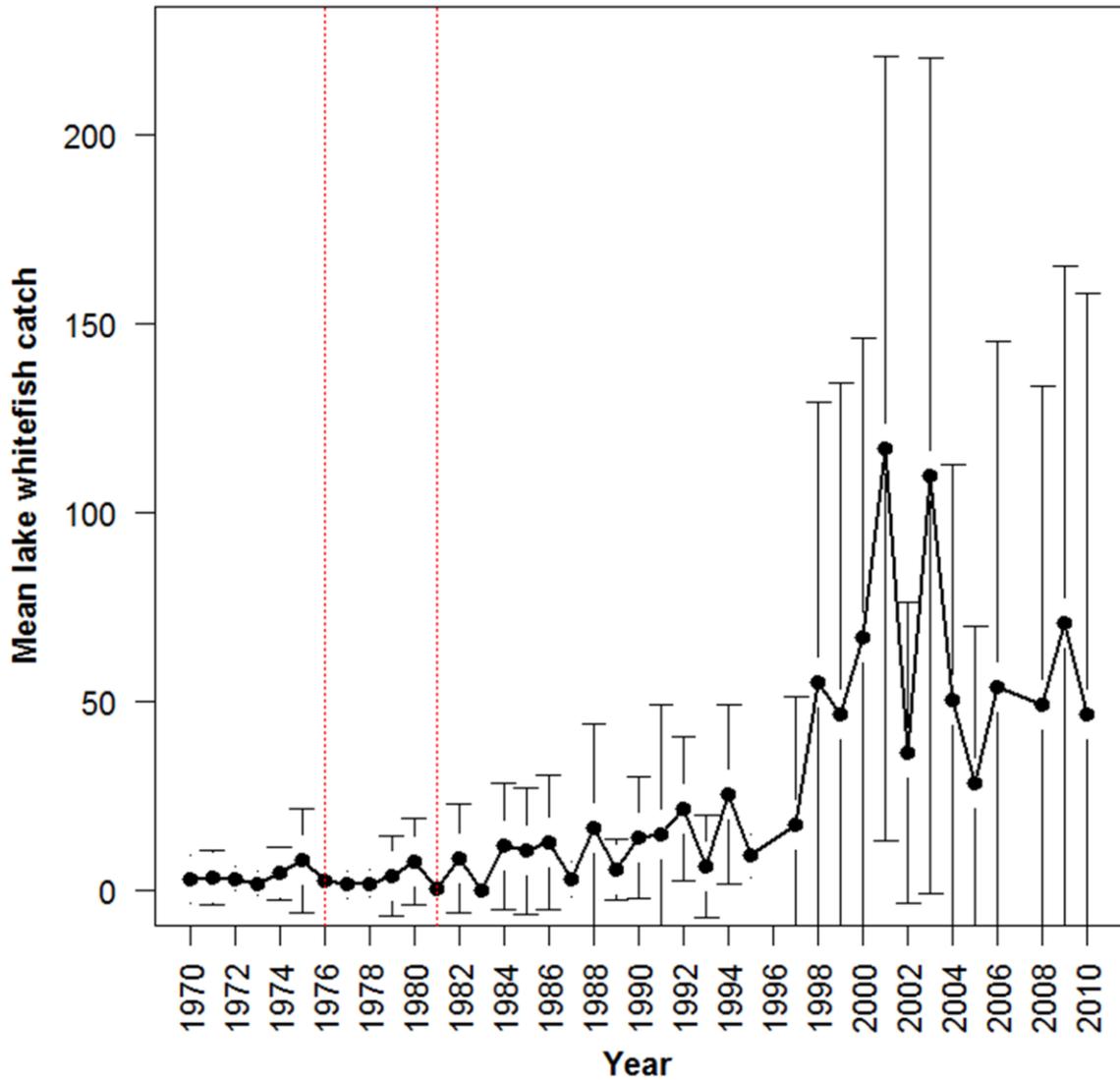
FIGURE 9. Annual mean lake whitefish (*Coregonus clupeaformis*) catch (+/- SD) from 1970 through 2010. The red dotted vertical lines correspond to establishment of the Gull Island Shoal Refuge (1976) and the Devils Island Shoal Refuge (1981). Data are included from all stations sampled by the Wisconsin Department of Natural Resources in the WI-2 management unit during the annual summer graded-mesh gill net survey. Data were not available for 1996 and 2007.

data collected inside versus outside of the refuges after both were implemented (1982-2010), the

next pattern to arise was that means of log-transformed lake whitefish catch appeared to be

consistently lower inside the refuges (Figure 10). The negative value of the refuge status

parameter estimated with the ANCOVA corroborated this observation (Table 5), despite direct

interpretation being complicated by the existence of an interaction term in the model. However,

the significant interaction between year and refuge status indicated that the slopes of the trends in

relative abundance were different for each treatment group, and the positive parameter estimate

(0.062) can be interpreted to mean that relative abundance inside of the refuge increased at a

greater rate than outside, which was consistent with a refuge effect. This analysis yielded

significant results overall (ANCOVA: $F = 113.2$; df = 3, 689; $P = < 2.2E\text{-}16$) and had an

adjusted R^2 value of 0.3272. This indicates that the lake whitefish model accounted for a greater

proportion of the variability in the catch data than the model developed for lake trout catch

(32.72%, as compared to, 13.18%).

Additionally, the trends in estimated lake whitefish relative abundance inside and outside

of the refuges were moving toward convergence (Figure 10). However, the individual annual

means in log-transformed observed catch in both treatment groups appeared to be changing in

reduced increments in recent years, with abundances calculated from stations inside the refuges

exhibiting decreases in the years since 2000 (Figure 10). This observation was also seen in the

data for the entire WI-2 management unit (Figure 9) and implies that some aspect of lake

whitefish population dynamics has shifted in recent years.

Cisco catch averaged annually for all the graded-mesh survey data in the WI-2

management unit shows increases in the decades after implementation of the two refuges (Figure

11). A high amount of variability is evident from year to year. Subsequently, the results of the

cisco analysis were less conclusive than for the other species I evaluated. Despite the
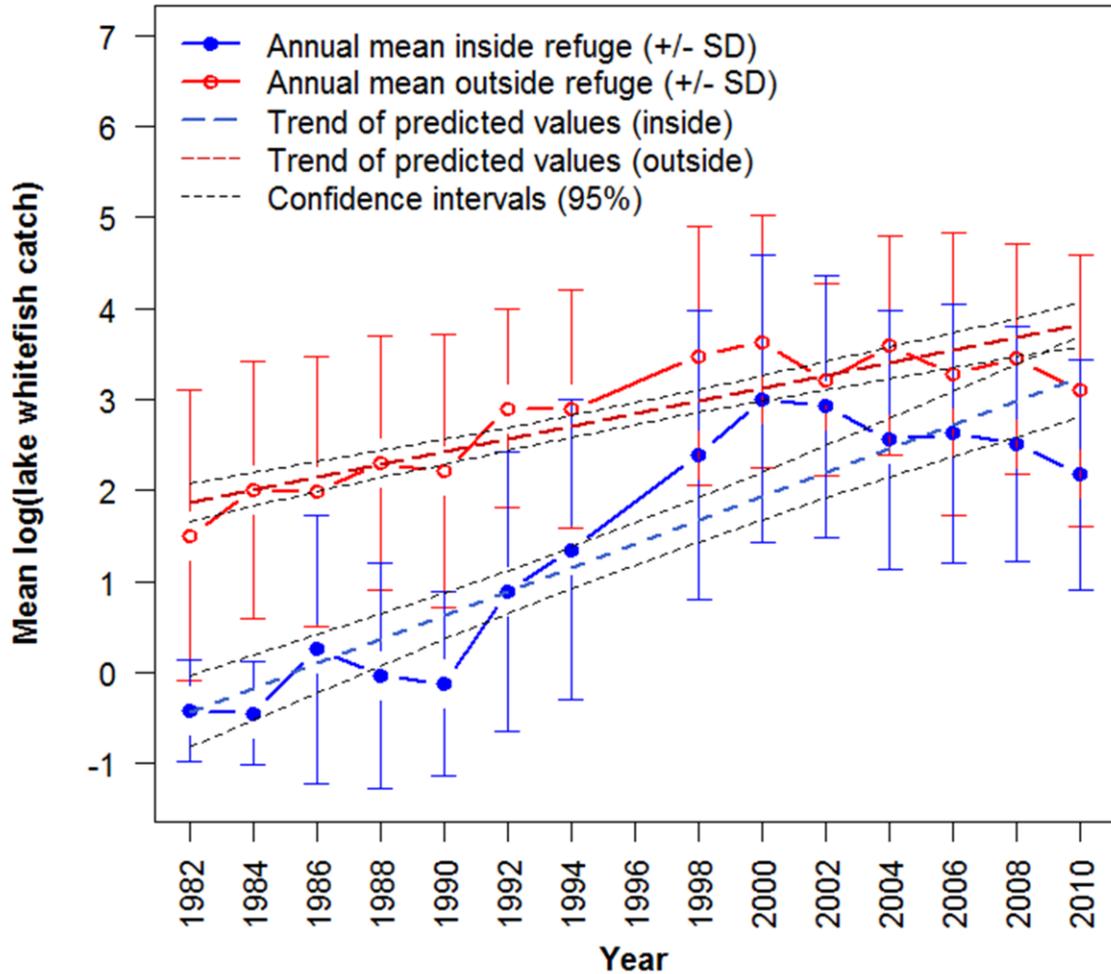
FIGURE 10. Annual log-transformed mean lake whitefish (*Coregonus clupeaformis*) catch against time, inside (blue with closed circles) vs. outside (red with open circles) of the refuges. The blue and red dashed lines are the predicted values of the model fitted with the parameter estimates in Table 5, and correspond to inside and outside of the refuges, respectively. Error bars are +/- one standard deviation (SD) from the annual means; the fine dotted black lines correspond to the 95% confidence intervals of the predicted values.

TABLE 5. Lake whitefish (*Coregonus clupeaformis*) linear model terms and associated ANCOVA parameter estimates. "Refuge status" corresponds to the treatment (inside refuge boundaries) and control (outside refuge boundaries) areas. Asterisks denote level of significance ($P \leq 0.001$***).

Model Term	Estimate	Standard error	P-value	
(Intercept)	-136.100	13.750	< 2E-16	***
Year	0.070	0.007	< 2E-16	***
Refuge status	-124.800	29.070	2.01E-05	***
Year × Refuge status	0.062	0.015	2.52E-05	***
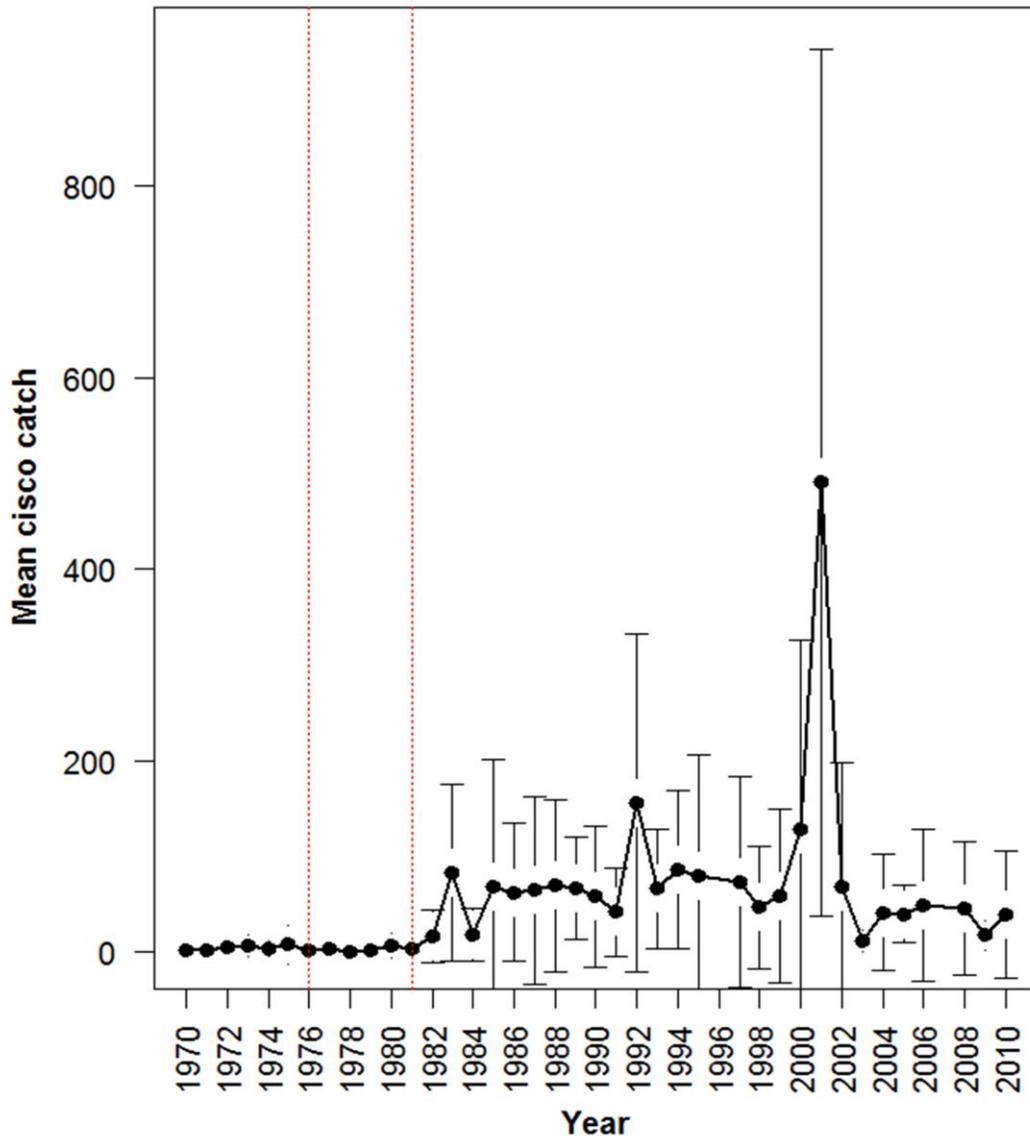
FIGURE 11. Annual mean cisco (*Coregonus artedi*) catch (+/- SD) from 1970 through 2010. The red dotted vertical lines correspond to establishment of the Gull Island Shoal Refuge (1976) and the Devils Island Shoal Refuge (1981). Data are included from all stations sampled by the Wisconsin Department of Natural Resources in the WI-2 management unit during the annual summer graded-mesh gill net survey. Data were not available for 1996 and 2007.

significance of the overall ANCOVA using data from even years since 1982, ($F = 7.992$; df $= 3$, 689; $P = 3.047\text{E-}05$), the adjusted R^2 value indicated that the model only accounted for 2.94% of the variability in the data. This is not surprising, considering that none of the model terms were

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statistically significant (Table 6). I therefore rejected the hypothesis that the slopes of the trends in cisco catch differed by treatment (refuge status). Since the interaction term was not significant, I also analyzed the main effects separately. The resulting ANCOVA demonstrated that only refuge status was significant, and after dropping the year and intercept terms from the model, a single factor ANOVA ($F = 805.5$; df = 2, 691; $P = < 2$E-16) yielded a significant refuge main effect that showed log-transformed catch to be greater outside of the refuges (mean = 3.035; standard error = 0.081) than inside (mean = 2.218; standard error = 0.154) overall. This result confirmed visual interpretation of the means depicted in Figure 12, aside from the population abundance spikes inside the refuges observed in 1986 and 2000.

Upon noticing that these spikes in cisco mean relative abundance appeared higher within refuge areas, I further investigated possible reasons for their magnitude. The first noticeable spike in the data after both refuges' implementation occurred in 1986 and could be due to a reportedly strong year class from 1984 recruiting to the population at this point and becoming vulnerable to the sampling gear (MacCallum and Selgeby 1987; Bowen et al. 1991). The distribution of cisco lengths collected in 1984 was consistent with this conclusion, due to the greater proportion of fish sampled with lengths from 200 to 250 mm (Figure 13), which is within the range of age-2 fish according to cisco lengths-at-age estimated by others (Ebener et al. 2008b; Yule et al. 2008; Stockwell et al. 2009). However, there was no obvious difference between the cisco lengths inside versus outside of the refuges, other than a slightly larger proportion of smaller fish (<200mm) found outside of refuge boundaries. The data from 2000 also demonstrated a notable spike in mean cisco catch (mean = 127.36; standard deviation [SD] = 199.16), that was likely due to the strong 1998 year class (Hoff and Gorman 2007), which appeared to be particularly well-represented within refuge boundaries (Figure 12). The fish lengths measured in 2000 were also consistent with this conclusion (Figure 14). The overall

TABLE 6. Cisco (*Coregonus artedi*) linear model terms and associated ANCOVA parameter estimates. "Refuge status" corresponds to the treatment (inside refuge boundaries) and control (outside refuge boundaries) areas.

Model Term	Estimate	Standard error	P-value
(Intercept)	-17.701	18.537	0.3400
Year	0.010	0.009	0.2640
Refuge status	-12.216	39.185	0.7550
Year × Refuge status	0.006	0.0196	0.7710
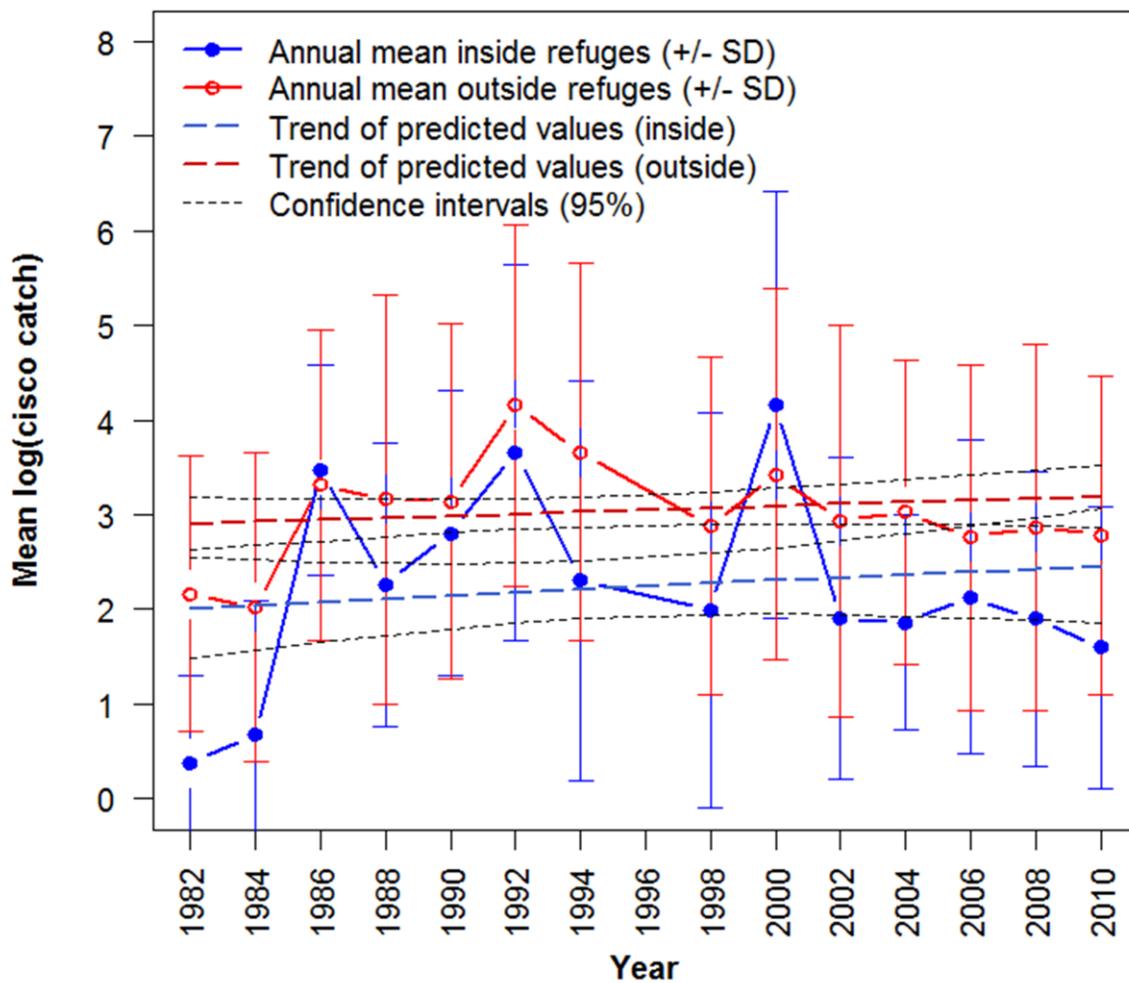
FIGURE 12. Annual log-transformed mean cisco (*Coregonus artedi*) catch against time, inside (blue with closed circles) vs. outside (red with open circles) of the refuges. The blue and red dashed lines are the predicted values of the model fitted with the parameter estimates in Table 5, and correspond to inside and outside of the refuges, respectively. Error bars are +/- one standard deviation (SD) from the annual means; the fine dotted black lines correspond to the 95% confidence intervals of the predicted values.

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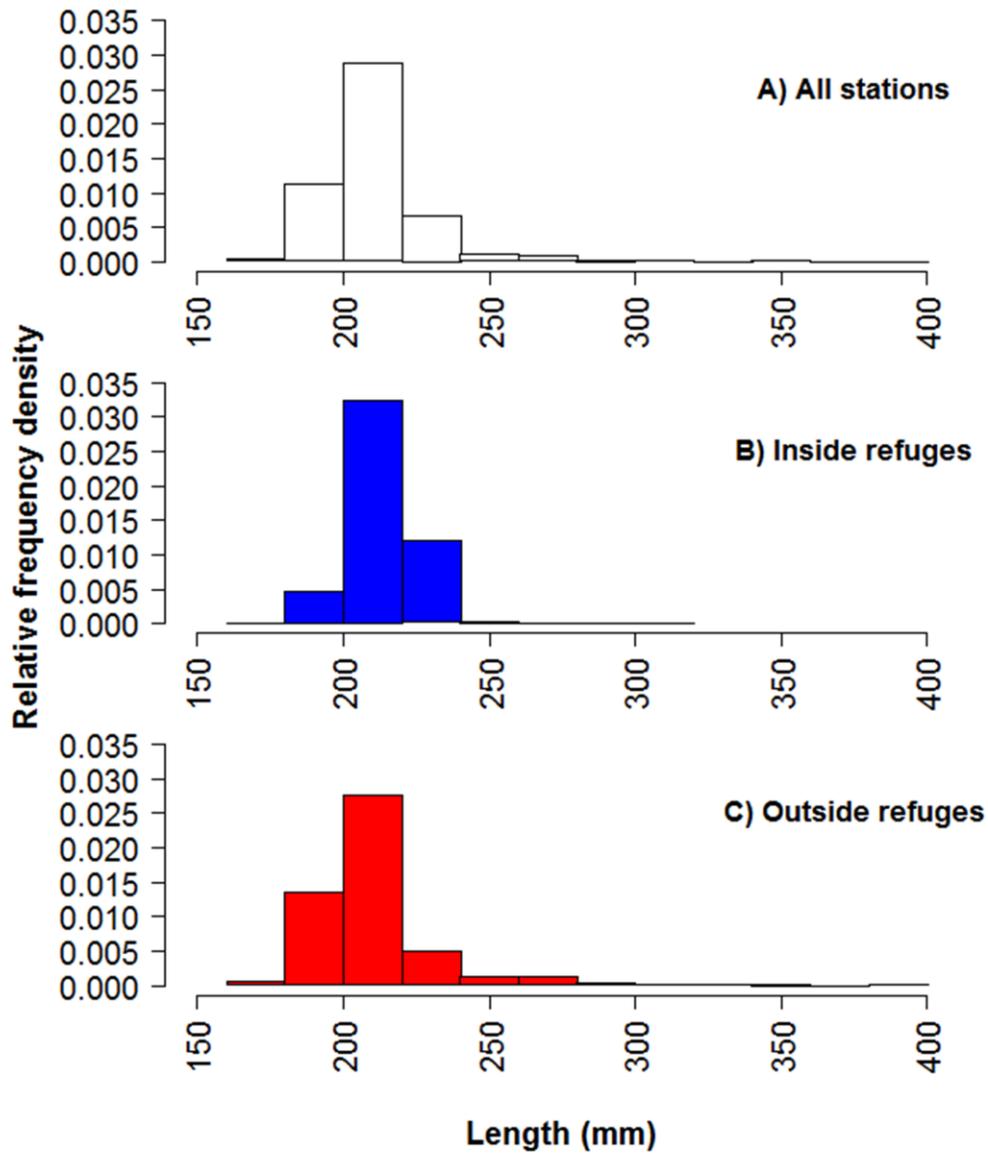
FIGURE 13. Length relative frequency densities exhibited in cisco (*Coregonus artedi*) collected during the 1986 summer index survey at: **(A)** all stations (white bars); **(B)** only stations located inside the refuges (blue bars); and **(C)** only stations located outside of the refuges (red bars). The area of each bar is equal to the relative frequency (proportion) of corresponding cisco lengths in the total sample.

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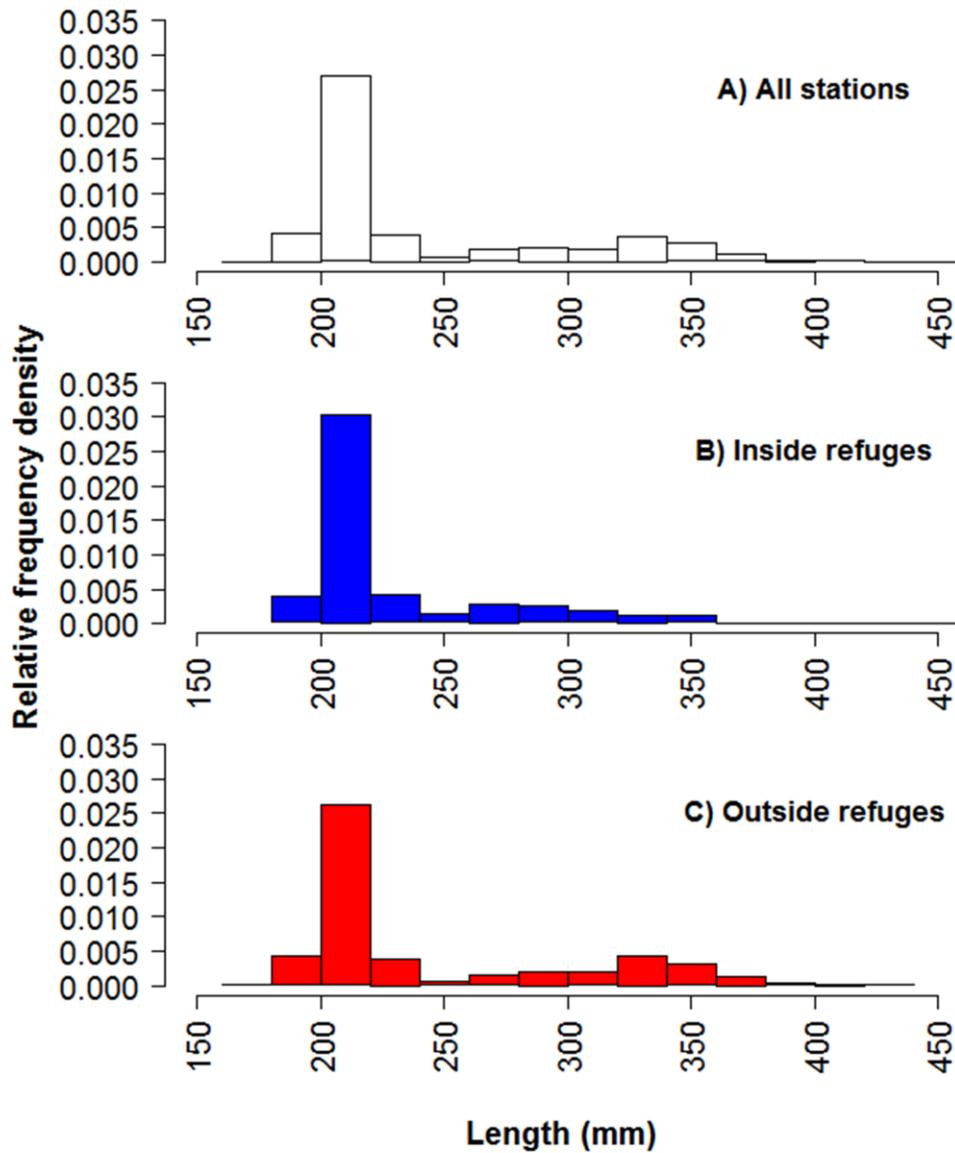
FIGURE 14. Length relative frequency densities exhibited in cisco (*Coregonus artedi*) collected during the 2000 summer index survey at: **(A)** all stations (white bars); **(B)** only stations located inside the refuges (blue bars); and **(C)** only stations located outside of the refuges (red bars). The area of each bar is equal to the relative frequency (proportion) of corresponding cisco lengths in the total sample.

distribution of lengths inside the refuge as compared to outside appeared to be slightly more

skewed toward shorter lengths (inside: mean = 229.79, SD = 41.334; outside: mean = 245.09; SD

= 57.32), while the distribution outside had a second mode in the $300 - 350$ mm size range

(Figure 14). These spikes in abundance were therefore likely a reflection of variations in the

amount of catch at different sites in certain years, and did not yield evidence suggestive of a

refuge effect. I was not able to investigate the inside-refuge component of the additional visible

spike in 2001 (mean = 490.6, SD = 457.59) from the series of annual mean counts for the whole

WI-2 unit (Figure 11), because data from stations within refuges were only sampled during even

years.

Lastly, a visual inspection of model residuals plotted against fitted values and the normal

quantile-quantile plots appeared to indicate that the regression assumptions of homogeneity of

variance and normal distribution of error were satisfactorily met. Plots of the model residuals

against time also lacked obvious, substantial patterns, which would suggest the model satisfied

the assumption of independence of errors. Results of the Durbin-Watson test indicated there

were minor autocorrelations present in the residuals of the models for stocked lake trout, lake

whitefish, and cisco; however, the level of autocorrelation was relatively weak, so it was not

included in the models.

DISCUSSION

My results suggest evidence of a refuge effect on relative abundances of lake trout and

lake whitefish in the Apostle Islands. This conclusion is attributed to the fact that CPUEs

compiled during the WDNR's summer index surveys for both species increased at a greater rate

inside the refuges' boundaries than outside from the period of 1982 through 2010. However, my

model involving variables of time and refuge status did not explain the fluctuations in cisco catch during the same times series.

My findings further corroborate the conclusions of previous investigations of lake trout populations in Lake Superior, and particularly within the Apostle Islands, that have also noted the potential role played by the lake trout refuges in rehabilitation success (Swanson and Swedberg 1980; Bronte et al. 1995a; Hansen et al. 1995; Schram et al. 1995; Hansen et al. 1996; Fabrizio et al. 2001; Pollock et al. 2007). While my study design did not allow me to infer a causal relationship between the refuges and overall increasing trends in fish abundance, my results indicate a significant correlation. Closer review of trends according to whether the lake trout were wild or stocked, also supported others' previous conclusions about the reduced role played by stocked lake trout in rehabilitation (Krueger et al. 1986; Hansen et al. 1995; Corradin et al. 2008), because indications of refuge-related effects were only evident in wild fish. The fact that trends for wild lake trout would be significantly different in refuges versus non-protected areas, while the declining trends in stocked lake trout were not distinguishable according to refuge status, is not surprising given the combination of cessation of stocking efforts in the area and the known reduced site fidelity of stocked fish (Krueger et al. 1986; Hansen 1996).

The study results also have additional implications for progress toward lake trout rehabilitation. Reductions in the extent of incremental increases within the series of annual means in lake trout relative abundance since 2000 could possibly indicate that the earlier evidence of density-dependence noted by Corradin et al. (2008) is continuing to occur. This hypothesis would be in agreement with previous findings about the effects of marine reserves in other systems, in which density-dependent dynamics have also been shown to impact species in protected areas through negative feedback loops involving compensatory processes or induction of a spillover effect due to resource limitations in the protected area (Sánchez Lizaso et al. 2000;

Botsford et al. 2009). While this study did not evaluate recruitment dynamics with the intention of assessing the potential for density-dependence, the methods and results of this study may provide a starting point for further analysis aimed at such a determination at a spatial and temporal scale that is consistent with assessment of refuge effects. The potential results of such an analysis would be especially timely for upcoming management assessments of restoration progress, considering various fishery managers' perceptions of what constitutes rehabilitated status for lake trout in specific areas. Certain criteria, such as that total mortality of lake trout must remain below 45% on an annual basis, have been met (Hansen 1996), and such mortality rates are likely sustainable assuming levels of fishing and sea lamprey mortality do not increase (Nieland et al. 2008). Wild lake trout are able to successfully reproduce and support recruitment rates that sustain their populations in Lake Superior (Hansen et al. 1995), and the population is generally considered rehabilitated in light of the evidence of density-dependence suggested by Corradin et al. (2008) for the WI-2 management unit. However, based on the conclusions of Bronte et al. (1995a) and Schram et al. (1995), the State and Tribes noted that density-dependent survival must also be demonstrated specifically within the vicinity of the Gull Island Shoal and Devils Island Shoal spawning reefs in order to determine lake trout as being restored in this particular management area (Wisconsin State-Tribal Technical Committee 2009). My results, therefore, suggest such processes may have been occurring in the refuges during the last decade, which could be further evaluated through future investigation of population dynamics within each individual refuge during this time series.

Implications regarding the role of refuges in lake trout management can also be discussed according to the potential mechanisms by which the refuges may enhance populations. If one considers spillover, described as when higher densities of predators inside of reserves can serve as a source of fishable biomass if they move to external areas (Russ and Alcala 1996; Sánchez

Lizaso et al. 2000; NRC 2001), then the increased abundance of lake trout within refuge boundaries relative to outside is important for bolstering numbers in adjacent areas. This assumed contribution has potentially occurred even though these fish have relatively large home ranges (see Kapuscinski et al. 2005 for distance estimates). Consideration of the impact of species mobility on the extent of reserve effectiveness is prevalent in the literature, especially when the predator is highly mobile and therefore not protected during lengthy travels beyond reserve boundaries (Shipp 2003; Hilborn et al. 2004; Botsford et al. 2009; Le Quesne and Codling 2009). However, Willis et al. (2003a) concluded that reserves can impact relatively mobile species regardless of whether individuals' behavior results in them remaining in the reserve vicinity only during spawning seasons or for longer periods of time. My results suggest that this situation is the case for lake trout, which complements the assertions of others (e.g., Pollock et al. 2007) that protection of spawning sites (such as those contained within the refuges in the Apostle Islands) would be an effective way of limiting fishing mortality on populations that spawn there. Not only are adult spawners protected during a vulnerable period, but once their eggs hatch, adjacent areas are provided with recruits via larval dispersal. At the same time, refuge effects may potentially be proportional to the amount of time individuals spend inside refuge boundaries.

The results of my analysis also contribute additional insight to the overall recovery of lake whitefish populations in the decades since refuge implementation. While there are a variety of additional management actions and environmental conditions that also likely contributed to this trend (Ebener 1997; Ebener et al. 2008a; Seider and Schram 2011), my results are consistent with the conclusion that the protection from harvest provided by the refuges is one of these contributing factors in the Apostle Islands region. This conclusion corroborates the inference

made by Seider and Schram (2011), who also note the potential importance of the lake trout refuges in protecting lake whitefish stocks from over-exploitation in this area.

Inferring whether the suggested refuge effect is necessarily prompted by a specific mechanism for lake whitefish is more complicated than with lake trout. Unlike lake trout, (who demonstrate higher mean CPUE inside the refuges on an annual basis), lake whitefish are found in lower numbers inside the refuges, which I hypothesize is due to a preference for habitats that happen to be outside the refuges. This preference could be reflective of the fact that, except for a couple productive sites along the southern end of the Devils Island Shoal Refuge, the majority of the known historic lake whitefish spawning sites were located near the islands and shoals not encompassed by the refuges (Coberly and Horrall 1980). Alternatively, this pattern could also be indicating a type of species interaction between lake whitefish and lake trout, because the higher numbers of lake trout in the refuges may be negatively affecting lake whitefish through competition or predation. However, an interaction based on direct predation is unlikely given the limited proportion of lake whitefish found in lake trout diets (1.2% of total biomass, according to stomach content analysis performed by the WDNR on lake trout sampled during the summer graded-mesh gill net surveys from 2001 through 2010). It may however, be worth investigating whether lake trout were limiting lake whitefish counts inside the refuges through predation or competition at some earlier life stage during different portions of the time series.

Regardless of these patterns and various possibilities for the conditions affecting lake whitefish distributions, the indication of a refuge effect attributed to the greater rate of increase in lake whitefish catch within refuge boundaries as compared to outside is of primary importance, because it is evidence that the refuges intended for lake trout also aided in lake whitefish rehabilitation. Since my analytical approach incorporated the variable of time with refuge status, I was also able to test for changes in relative abundance despite the spatial

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distribution of lake whitefish habitat. This approach was based on the assumption that physical

habitats (e.g., bottom depth and substrate) could not have undergone significant refuge area-

specific changes within the study's time span. Therefore, I can infer this increasing trend in lake

whitefish catch is correlated with refuge status, possibly due to the reduced fishing mortality

afforded through the refuges' protection. Additionally, similar to conclusions noted in the above

discussion of the extent of reserve effects when species mobility is considered, lake whitefish

appear to benefit from protection regardless of any potential movements outside of refuge

boundaries.

The deviations between the predicted trendlines and the annual means in log-transformed

observed catch in both treatment groups during periods in the late 1990s and the last couple of

years (Figure 9) could indicate that the model used to fit the data might not be ideal for use in

future predictions of lake whitefish CPUE. While it is true that no model will ever fit the

observed data perfectly, alternative analytical approaches (e.g., generalized linear mixed models)

provide greater flexibility in accounting for error structures within historical datasets (Venables

and Dichmont 2004), and future research could explore these options if enhanced predictive

capabilities are desired. Regardless, for this study's objectives, the linear model I used proved

effective as an explanatory model for identifying potential refuge effects over the last several

decades, which was my original intent. Furthermore, the reduced rate of change observed

between sequential annual means of lake whitefish relative abundance in both the protected and

non-refuge areas in recent years (Figure 9) could also be indicative of density-dependence, which

would be consistent with a theory presented by Seider and Schram (2011) after observing

declines in growth parameters of lake whitefish in the Apostle Island since 2002. This would be

a continuation of the reductions in growth (mean maximum length) during the 1980s and 1990s

that was also attributed to density-dependence resulting from the increased amount of lake

whitefish in the region beginning in the late 1970s (Bronte et al. 2003), therefore signifying additional progress towards rehabilitation. Similarly, as lake whitefish reach higher relative abundances, and therefore higher densities, inside the refuges they would be more likely to move to external areas and become available to promote fishery production in the Apostle Islands.

In order to further evaluate whether density-dependent processes are more pronounced within the refuges, fish length could be included as the dependent variable in a linear model, once again with time as a covariate to refuge status. Length, as a way of measuring growth rates and possible age structure, is also another common metric used in marine reserve evaluations (Sánchez Lizaso et al. 2000; Willis et al. 2003a; Nowlis and Friedlander 2004). The graded-mesh gill net survey data include a large proportion of length measurements on the sampled lake trout, and a limited number of lengths for lake whitefish and cisco. Subsequently, a preliminary investigation I conducted of the differences between the trends in mean lengths according to refuge status suggested that lake trout and lake whitefish demonstrated different mean lengths inside versus outside of the reserves, with some changes in the slope of the trajectories in more recent years. Depending on the magnitude and direction of the effect, such patterns could be further suggestive of density-dependent processes due to reductions in exploitation, depending on the population's stage of recovery (Sánchez Lizaso et al. 2000; Abesamis and Russ 2005). Further investigation of these possibilities could help determine if an additional indication of population rehabilitation (i.e., density-dependence as suggested by Bronte et al. 1995a) was occurring in recent years for lake trout or lake whitefish, and whether it was happening at a faster rate within refuge boundaries.

I originally expected that my evaluation of trends in relative cisco abundances would demonstrate some indication of an indirect refuge effect due to predation from increasing numbers of lake trout within refuge boundaries. However, despite the fact that ciscoes were

generally found in lower numbers inside the refuges, my results did not suggest existence of statistically significant indirect refuge effects on trends in abundance over time. While this might be due to the fact that the refuges have *actually not* been impacting cisco populations, the high amount of variability exhibited in the cisco data may obscure this analysis. Cisco are a difficult species to monitor accurately because of the combination of strong year class variability, shifts between pelagic and benthic orientation according to sex and life history stage, and limitations in selectivity of survey gear for this species (Stockwell et al. 2006; Stockwell et al. 2009; Yule et al. 2006). While a combination of gears and methods may be preferable for more accurate estimates, I originally felt the WDNR's use of the summer index survey data in fish community analyses indicated it was a satisfactory choice for this analysis, even though it was not targeted specifically at cisco. However, difficulties in species identification of the other cisco species (e.g., bloater, shortjaw, and kiyi) and cisco (i.e., lake herring) led the WDNR to report annual indexes grouped according to broader taxa (Seider 2010). Discussion of these difficulties in distinguishing between coregonine species exist in the literature, especially among the deepwater ciscoes, also known as chubs (Dryer and Beil 1964; Lawrie and Rahrer 1972), which could have affected the accuracy of cisco abundance data I analyzed.

However, despite the lack of statistically significant evidence for a possible refuge effect on cisco abundances, observing the raw data patterns could still point toward hypothetical interactions with lake trout in the Apostle Islands. The overall lower abundance of ciscoes inside of the refuges may be linked to the greater number of lake trout found in those areas. Additionally, while I can only speculate at this time, the instances of supposed deviations from the general trends in abundances inside versus outside of the refuges in one species seem to lag behind the other. For example, there is a decrease in annual mean lake trout catch inside the refuges and an increase in mean counts outside in 1998 which quickly reverses again by 2000

(see Figure 4). There is also a sharp increase in mean cisco catch inside the refuges in 2000 (Figure 12) which could suggest that predator-prey dynamics may be impacting fish movement at a scale that is noticeable in this summer index survey data relative to refuge extent. If such a dynamic was happening in recent years, it could be further investigated through assessment of whether the large increase in cisco relative abundance in 2001 (Figure 10) was distributed differently between refuge and non-refuge areas (if such data were available), and whether the areas demonstrating high lake trout abundances also seemed to shift, perhaps to enhance foraging success.

Few assessment models for reserve effects address trophic dynamics or the entire fish community (Pelletier et al. 2008). I attempted to begin to evaluate whether such interactions were occurring in the Apostle Islands, but the lack of statistically significant results (at a 5% level of significance) makes it difficult to conclude that this is worth pursuing with this methodology. However, alternative analytical approaches might be better suited to testing such questions in the future. One way to assess whether trophic dynamics were affected by refuge status would be to further evaluate the diet data for corresponding lake trout in this dataset. Then, one could test for a progression in the annual amounts and sizes of ciscoes in lake trout diets during this time series, and whether any correlations existed between diets consumed by lake trout captured in protected versus non-protected areas. Additionally, consideration of additional members of the fish community would further address other interactions and the role of the refuges in fish community shifts. For example, a recent analysis completed near the Northern Refuge for lake trout in Lake Michigan concluded that burbot predation on lake trout could be affecting progress toward lake trout rehabilitation (Jacobs et al. 2010). While Schram et al. (2006) did not show evidence of this type of interaction in Lake Superior, assuming instead that increased lake trout numbers may be limiting burbot populations, they also did not evaluate

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the data with refuge status as a variable to test if predator-prey dynamics shifted when analyzed in the theoretical absence of fishing mortality. Therefore, the most immediate way to further assess the potential for this type of interaction in the study area would be to evaluate trends in burbot catch in and out of the refuges in Lake Superior. Despite the fact that overall burbot numbers have declined in the Apostle Islands since implementation of the refuges (Schram et al. 2006), testing for a refuge effect over time may yield detectable patterns in relative abundances at a finer refuge-specific scale. Depending on the direction and magnitude of these trends, such results could corroborate theories about burbot and lake trout interactions. Additionally, given the known shifts in community structure related to rainbow smelt declines coupled with general cisco increases and shifts in lake trout diets (Bronte et al. 2003; Gorman 2007; Ray et al. 2007), future research efforts should focus on further evaluation of these changing dynamics when analyzed with refuge status as a possible effect. If indications of such dynamics were apparent, additional research should be focused on determination of whether food web structure or trophic interactions were impacted by reserve designation. Such an objective would require substantial diet analyses and possible tracking of stable isotope ratios through trophic levels (Harvey and Kitchell 2000). Additionally, an ecosystem modeling approach, such as that developed for MPAs by Watson et al. (2000), could further predict potential effects of reserve implementation on trophic groups within the fish community.

Broad-scale implications and conclusions

The implications of my results suggesting the existence of refuge effects on relative abundances of lake whitefish and lake trout (especially those that are wild) prompts the conclusions that these refuges have potentially valuable benefits, and that improved understanding of their role in rehabilitation efforts and sustaining fish populations can be gained

through further study. Any remaining questions about reserve efficacy or inabilities to yield statistically significant results in favor of reserve effects for certain species, do not necessarily mean reserves lack effectiveness. In general, the absence of discernible reserve effects could mean they simply were not yet measureable, and that more time must pass before recovery in target fisheries becomes evident, such as a period spanning several generations of the targeted species. While this statement is not meant to imply that an obviously ineffective reserve should be kept in place unnecessarily, it does warn against premature assumptions about reserve functionality. Additionally, there are still other noteworthy values for consideration that may be associated with refuges. Many of these depend on the ethics governing one's perception of the primary reason for protecting an area, in the first place. An in-depth discussion of this nature would also necessitate a review of common conservation ethics as they relate to fisheries management (Callicott 1991; Krueger et al. 1995), as well as consideration of the wilderness concept and the relationship of humans with pristine natural areas (Nelson 1998, 2005) as it relates to aquatic environments (Sloan 2002). However, my opinion is that these lake trout refuges, both in Lake Superior and throughout the other upper Great Lakes, need to be maintained and studied further – for reasons including their potential utilitarian purpose, possible unknown or unnoticed effects, as well as for their intrinsic value.

There are also additional roles reserves can play in fisheries management, beyond the direct effects of potentially rebuilding fish stocks or increasing fisheries productivity. For instance, they can serve as a reference site, theoretically only impacted by natural mortality, for use in fisheries-related research and stock assessments in the absence of variability and uncertainty induced through estimation of fishing mortality (Stanley et al. 1987). They can also be used as part of a system-wide adaptive ecosystem-based management framework, such as through aiding in establishment of target reference points or performance indicators for stock

assessments (Babcock and Pikitch 2004). In addition, recent models demonstrate reserves may aid in development of alternative estimation of control roles used to evaluate fisheries management strategies, in which the ratio of fish density between reserve and non-reserve areas is used instead of the customary percentage of spawning stock biomass theoretically retained from fishing mortality exposure (Babcock and MacCall 2011). Given the potential refuge effects this study observed in lake trout and lake whitefish, two common species of importance for fisheries management, further evaluation of these reserves is therefore warranted, as they may be useful for such purposes beyond rehabilitation efforts.

On yet another level, one must also consider the effects the future may have on these reserves. None of the implications discussed thus far take environmental change or degradation into account. It is important to be aware of the impacts external environmental factors may exert on the intended function of a reserve. Degraded habitat linked to hypoxia or excessive sedimentation can render areas unsuitable for fish – either for their general movement patterns or during specific life stages, such as spawning. Given temperature changes already exhibited in the Great Lakes region, in addition to the future projections of climate change and the implicit alterations to local weather patterns and lake thermal structure, the extent of available fish habitat will likely shift (Lynch et al. 2010). It is therefore possible that the location of protected areas will either no longer be able to serve their intended purpose, or will be rendered unnecessary in situations where the fish community has shifted in ways that call for alternative fisheries management goals (e.g., the need for a larger prey-base to support expanded ranges of valuable predatory sportfish). Therefore, both current management and future planning of reserves must take such changes into account (Soto 2001). Such an approach could mean the concept of dynamically designed reserves would need to be implemented. This idea of reserve zoning to allow for shifting conditions has already been mentioned as a potential tactic in terrestrial (Peters

and Darling 1985; Bengtsson et al. 2003) and marine (Soto 2001) systems, and may need to become a reality in the Great Lakes should conditions require it.

As evidenced by the conclusions regarding the potential effectiveness of the lake trout refuges presented above, the projected impacts of environmental change, and the large extent of controversy surrounding MPA implementation and use, the pure existence of no-take reserves are not a cure-all for achieving sound conservation practices in fisheries sustainability (Allison et al. 1998; Agardy et al. 2003; Hilborn et al. 2004; Hedges et al. 2010; Agardy et al. 2011). Their demonstrated benefits imply that reserves cannot simply be dismissed, but it is important to remember that they are one of many tools at natural resource managers' disposal; they should be used in concert with other management actions specifically designed for each case at hand. They also do not exist in a vacuum – there is a whole suite of effects due to ecological, social, cultural, economic, and political conditions that can impact reserve performance and how well it is received by human communities (Pollnac et al. 2010). Management agencies' and the public's perceptions of reserves are therefore important aspects to consider when attempting an assessment of their efficacy (Christie *et al.* 2009). The restriction of stakeholder activities, especially those within the commercial, recreational, and subsistence fishing sectors, creates controversy that complicates policy decisions for fisheries management. In addition, other ecological factors (e.g., habitat and prey availability) affecting fish stocks make it increasingly difficult to gauge the role played by reserves in facilitating fisheries rehabilitation efforts or increasing fisheries sustainability, further complicating perceptions of their use and value. The vast range of conflicting opinions surrounding the use of reserves can hinder progress in their future effectiveness as a conservation and management tool (Agardy et al. 2003). This controversy is especially active in the aquatic realm because the oceans were historically viewed as part of the commons (Sloan 2002), and restrictions on the use of fisheries resources through

implementation of reserves can have drastic implications on the humans who relied on those areas and resources to satisfy economic, cultural, or nutritional needs (Gray 2010). Similarly, a lack of public consensus on the use of no-take fishing zones in fisheries management efforts may impact the level of agency attention and support of refuge assessment, including their ability to perform related research, monitoring and outreach projects. The only way to begin to approach solutions involving these types of issues is in an integrated manner that allows for overt consideration of the ecological and socio-political complexity associated with management actions (Hughes et al. 2005; Liu et al. 2007). Reserves exist within a system composed of an interacting web of feedback loops from different sectors; therefore we cannot assume they will be fully understood without considering the greater context in which they operate.

The scope of my evaluation of the lake trout refuges in the Apostle Islands, as well as the discussion of marine reserve efficacy, was limited to the context of fisheries rehabilitation and sustainability. I acknowledge there are other reserve objectives (e.g., conservation of cultural heritage) that require different forms of discourse and analytical approaches for evaluation. However, within the framework of fisheries, the explanatory model I used to evaluate trends in relative abundance of select species according to protection from harvest suggested the refuges are having an effect. This evidence supports conclusions that the increases in relative abundance of wild lake trout, and also lake whitefish, have been enhanced by the existence of the refuges over the last several decades, and that the refuges may continue to serve a purpose in bolstering populations of fishes beyond the original target species.

APPENDIX

Mapping of Lake Superior lake trout refuges

A geo-referenced digital map of the lake trout refuges in Lake Superior did not exist prior to this study. The most detailed map of the refuges available was published in the Wisconsin Department of Natural Resources (WDNR) fishing regulations (WDNR 2011). Discussion with WDNR staff confirmed that it was not geo-referenced. Therefore, I created maps of the refuges according to the boundaries identified and described in available government documents, which also required interpolation of bathymetric features needed for delineation of specific boundaries. All map preparations, analyses, and creation of refuge polygons were completed using ArcGIS version 10 (ESRI 2011).

The primary sources for the latitude and longitude coordinates and reference points defining the refuge boundaries were the map pictured in the WDNR fishing regulations (WDNR 2011) and the descriptions in the Wisconsin State Administrative Code (Wis. Admin. Code NR 26.23, Oct. 2010). I also obtained base layers and bathymetric data from a variety of sources, including the Great Lakes GIS project (see Great Lakes GIS (2005), for description), the National Oceanic and Atmospheric Administration (NOAA), the WDNR, and the Environmental Systems Research Institute (ESRI). These data provided the spatial information needed to refine locations of the landmarks and boundaries described in the fishing regulations and administrative code. The refuge maps created in this study all used the WTM83, NAD83 (1991) coordinate reference system, the standard also used by the WDNR. According to the WNDR's GIS Services Section website, this reference system is described as the "Wisconsin Transverse Mercator coordinate system of 1983 based on the 1991 adjustment to the North American Datum of 1983" and has also been previously referenced as "WTM83/91" (WDNR 2008).

The northern edge of the Devils Island Shoal Refuge boundary and a licensed commercial fishing zone within the Gull Island Shoal Refuge were defined according to a depth contour of 35 fathoms (210 ft. or 64 meters). However, owing to a lack of bathymetric data for Lake Superior depicting this particular depth contour, I estimated its location from existing bathymetric data in order to define these refuge boundaries. Since those potentially fishing in the open waters of the Apostle Islands would likely use navigational data and charts provided by NOAA, I decided that basing these refuge boundaries on NOAA depth soundings would yield maps that were more relevant to those users most impacted by the refuges' locations. Additionally, enforcement staff would also likely use the same navigational information to determine if fishermen were in the appropriate areas while at sea.

I obtained these data from NOAA's Electronic Navigational Charts® (NOAA ENCs) website. I then interpolated the point depth soundings into a raster format via the inverse distance weighted (IDW) method available in the Spatial Analyst Extension of ArcMap (ESRI 2011). I then created contours from the resulting layer by using the contour tool also available in ArcMap's Spatial Analyst Extension. I selected the contour closest to 64 m, and used this to trace the relevant refuge boundaries, which are depicted in Figure 15. These are the refuge boundaries and set of bathymetric contours I used for all subsequent analysis. However, it should be noted that a limitation of this approach is the course resolution of the bathymetric data, and so interpolated contours do not necessarily represent true depths at each location. For increased precision and accuracy of future analyses, refuge boundaries should be constructed using bathymetric data of higher resolution, such as accurate to a single meter, should such data become available.
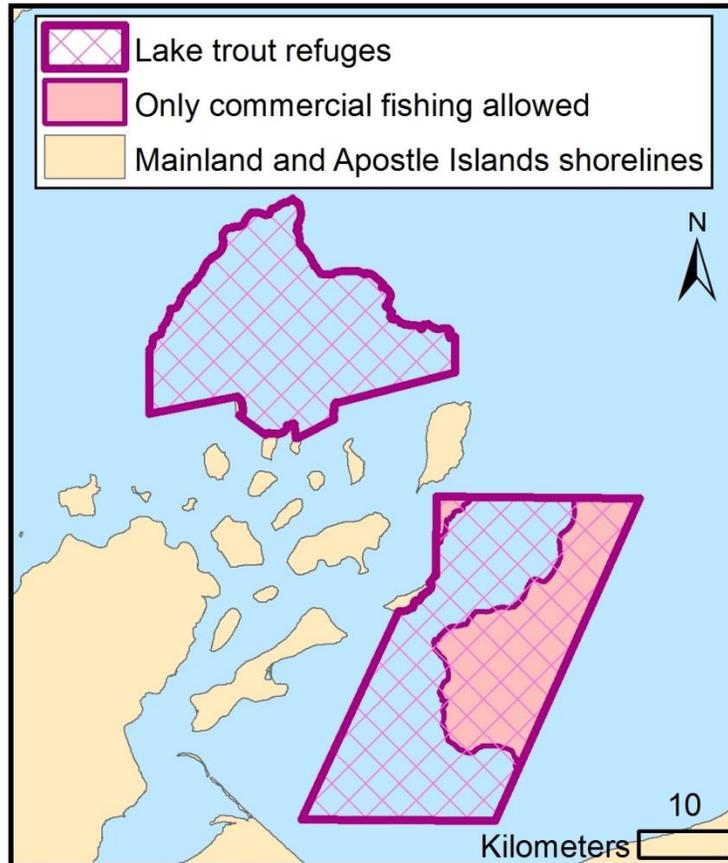
FIGURE 15. Lake trout refuges in the Apostle Islands area of Lake Superior with boundaries defined by a 64 meter contour interpolated from depth soundings obtained from the National Oceanic and Atmospheric Administration (NOAA). Crosshatching indicates the full extent of the refuges, and the pink shaded area is the region open only to licensed commercial fishing. Additional base layer data sources are listed below.

While not represented on any of the published maps of refuges, there were also a variety of specific exceptions defined within the State Administrative Code (Wis. Admin. Code NR 26.23, Oct. 2010) for single-species fisheries within the Gull Island Shoal Refuge. These exceptions included an open area for a month-long (November 5 – December 6) Menominee whitefish season adjacent to Michigan Island out to a depth of 7 fathoms (12.8 m) and a month and a half-long (November 1 – December 15) cisco season at depths shallower than 25 fathoms (45.7 m). I defined these boundaries according to the bathymetric contours computed from NOAA data that were closest to these values. These zones are all depicted in Figure 16, along

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with the gill net survey locations used in the study's evaluation of refuge effects. Some stations defined as being inside the refuges were within the zone open to the cisco fishery. This result implies that I cannot assume that ciscoes were protected from fishing mortality at all times within the refuges.

In addition to the basic refuge boundaries and various zones described above, there were also special use rules defining areas for tribal fishing within the refuges according to the 2005 State-Tribal Agreement for Lake Superior (WDNR et al. 2005). Since none of these zones appeared in published maps of the refuges and were not referenced in any of the published literature I reviewed, I did not digitize them prior to this study's analysis. However, such maps should be created for use in future evaluations of refuge extent and determination of overlap with fish survey stations.
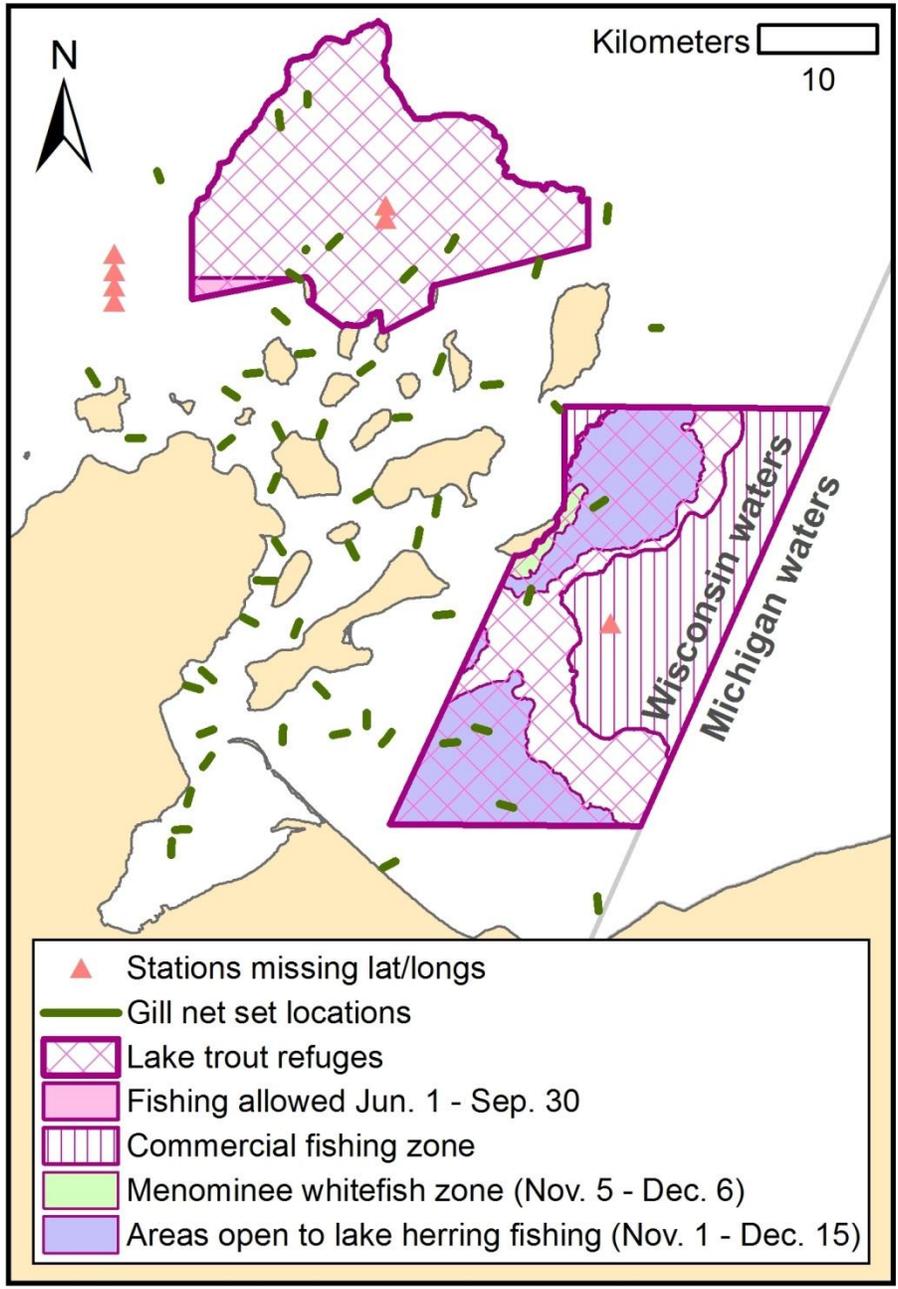
FIGURE 16. Lake trout refuges in the Apostle Islands, Lake Superior, as described in the Wisconsin State Administrative Code. Full refuge extent is indicated by the purple line surrounding cross-hatching. Licensed commercial fishing is allowed in the zone indicated by vertical simple-hatch, and commercial and recreational fishing is allowed during the summer months in the pink shaded area. A zone open to cisco fishing within the Gull Island Shoal Refuge is indicated by the purple shaded area; an open zone for Menominee whitefish fishing is indicated by the light green shaded area. Locations of gill net stations used for the study during even years are indicated by dark green lines. Stations missing coordinates but identified by the WDNR as being located inside or outside of the refuges are indicated by orange triangles and are not representative of exact locations. Additional base layer data sources are listed below.

Additional source information for map layers

Harbor approach soundings for Apostle Islands region. Sounding Feature, shapefile. (2011). Extracted from NOAA's Electronic Navigational Charts® (NOAA ENCs) Direct to GIS Web Portal. (October, 2011). Available: http://www.nauticalcharts.noaa.gov/csdl/encdirect_download.html

Lake Superior Medium Resolution Digital Shoreline. ls_shore_NOAA_70k, shapefile. (1992). Produced by the National Oceanic and Atmospheric Administration (NOAA), Office of Ocean Resources, Conservation and Assessment, Strategic Environmental Assessments Division. Supplied by the Great Lakes GIS project of the University of Michigan and Michigan Department of Natural Resources (MDNR), Institute for Fisheries Research (IFR), Ann Arbor, Michigan, USA (March, 2010).

Lake Superior bathymetry contours (50-m intervals). ls_cnt_50m_IFR, shapefile. (2006). Produced and Supplied by the Great Lakes GIS project of the University of Michigan and MDNR, IFR, Ann Arbor, Michigan, USA (March, 2010).

Lake Superior bathymetry (1000-m resolution). ls_bath_1km, raster dataset. (1998). Produced by Natural Resources Research Institute, University of Minnesota, Duluth. Supplied by the Great Lakes GIS project of the University of Michigan and MDNR, IFR, Ann Arbor, Michigan, USA (March, 2010).

Lake Superior fishery management units. ls_laketrout_mgmt_units_IFR, shapefile. (2007). Supplied by the Great Lakes GIS project of the University of Michigan and MDNR, IFR, Ann Arbor, Michigan, USA (March, 2010).

lake_superior_bathymetry (20 m intervals; unknown origin). Lk_Superior_Bathymetry_wtm, shapefile. (publication year unknown). Downloaded from the Great Lakes Information Network's "Maps and GIS of the Great Lakes Region" website (July 2010). Available: http://gis.glin.net/ogc/services.php#lake_superior_bathymetry

Michigan's Great Lakes Waters. MI_GLwaters_IFR, shapefile. (2006). Produced and Supplied by the Great Lakes GIS project of the University of Michigan and MDNR, IFR, Ann Arbor, Michigan, USA (March, 2010).

Navigational Chart 14973 for the Apostle Islands, Region 22. 14973_1, raster image in BSB format. (2010). Obtained from NOAA as a Raster Navigational Chart (NOAA RNCs™). (December, 2010). Available: http://www.nauticalcharts.noaa.gov/mcd/Raster/index.htm.

Provinces, Canada. ON_province_ESRI_100k, shapefile. (2001). Produced by the Environmental Systems Research Institute, Inc. (ESRI). Supplied by the Great Lakes GIS project of the University of Michigan and DNR, IFR, Ann Arbor, Michigan, USA (March, 2010).

Region 22 depth soundings. Sounding Feature, shapefile. (2010). Obtained from NOAA as Electronic Navigational Charts® (NOAA ENCs) in S-57 format and converted into shapefiles using the Electronic Navigational Chart Handler extension. (July, 2010). Available: http://www.charts.noaa.gov/ENCs/ENCs.shtml

State boundaries, United States. GLB_states_ESRI_100k, shapefile. (2000). Produced by ESRI. Supplied by the Great Lakes GIS project of the University of Michigan and MDNR, IFR, Ann Arbor, Michigan, USA (March, 2010).

Wisconsin shoreline and Apostle Island outlines. wisppolyx,shapefile. (publication year unknown). Provided by the WDNR and reportedly derived from the U.S. Geological Survey (USGS) 1:2,000,000-scale Digital Line Graphs (DLGs) (April, 2010).

WTM83/91 ArcGIS Projection File. NAD_1983_HARN_Transverse_Mercator, projection. (2009). Developed and supplied by the WDNR (June, 2010). Available: http://dnr.wi.gov/maps/gis/wtm8391.html.

LITERATURE CITED

LITERATURE CITED

Abell, R., J. D. Allan, and B. Lehner. 2007. Unlocking the potential of protected areas for freshwaters. Biological Conservation 134(1):48-63.

Abesamis, R. A., and G. R. Russ. 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecological Applications 15(5):1798-1812.

Agardy, T., and coauthors. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. Aquatic Conservation-Marine and Freshwater Ecosystems 13(4):353-367.

Agardy, T., G. Notarbartolo di Sciara, and P. Christie. 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Marine Policy 35(2):226-232.

Alcalá, R. E., and C. A. Domínguez. 2005. Differential selection for carnivory traits along an environmental gradient in *Pinguicula moranensis*. Ecology 86(10):2652-2660.

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8(sp1):S79-S92.

Babcock, E. A., and A. D. MacCall. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? Canadian Journal of Fisheries and Aquatic Sciences 68(2):343-359.

Babcock, E. A., and E. K. Pikitch. 2004. Can we reach agreement on a standardized approach to ecosystem-based fishery management? Bulletin of Marine Science 74(3):685-692.

Babcock, R. C., and coauthors. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences 107(43):18256-18261.

Baskett, M. L., F. Micheli, and S. A. Levin. 2007. Designing marine reserves for interacting species: Insights from theory. Biological Conservation 137(2):163-179.

Bengtsson, J., and coauthors. 2003. Reserves, resilience and dynamic landscapes. Ambio 32(6):389-396.

Botsford, L., and coauthors. 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Reviews in Fish Biology and Fisheries 19(1):69.

Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications 13(sp1):25-31.

Bowen, S. H., D. J. D'angelo, S. H. Arnold, M. J. Keniry, and R. J. Albrecht. 1991. Density-dependent maturation, growth, and female dominance in Lake Superior lake herring (*Coregonus artedii*). Canadian Journal of Fisheries and Aquatic Sciences 48(4):569-576.

Bronte, C. R. 1993. Evidence of spring spawning lake trout in Lake Superior. Journal of Great Lakes Research 19(3):625-629.

Bronte, C. R., and coauthors. 2003. Fish community change in Lake Superior, 1970–2000. Canadian Journal of Fisheries & Aquatic Sciences 60(12):1552-1574.

Bronte, C. R., and coauthors. 2007. Relative abundance, site fidelity, and survival of adult lake trout in Lake Michigan from 1999 to 2001: Implications for future restoration strategies. North American Journal of Fisheries Management 27(1):137-155.

Bronte, C. R., S. T. Schram, J. H. Selgeby, and B. L. Swanson. 1995a. Density-independent survival of wild lake trout in the Apostle Islands area of Lake Superior. Journal of Great Lakes Research 21(sp1):246-252.

Bronte, C. R., S. T. Schram, J. H. Selgeby, and B. L. Swanson. 2002. Reestablishing a spawning population of lake trout in Lake Superior with fertilized eggs in artificial turf incubators. North American Journal of Fisheries Management 22(3):796-805.

Bronte, C. R., J. H. Selgeby, J. H. Saylor, G. S. Miller, and N. R. Foster. 1995b. Hatching, dispersal, and bathymetric distribution of age-0 wild lake trout at the Gull Island Shoal complex, Lake Superior. Journal of Great Lakes Research 21(sp1):233-245.

Callicott, J. B. 1991. Conservation ethics and fishery management. Fisheries 16(2):22-27.

Claudet, J., and P. Guidetti. 2010. Improving assessments of marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems 20(2):239-242.

Coberly, C. E., and R. M. Horrall. 1980. Fish spawning grounds in Wisconsin waters of the Great Lakes. University of Wisconsin Sea Grant Institute, WIS-SG-80-235, Madison, WI.

Corradin, L. M., M. J. Hansen, D. R. Schreiner, and M. J. Seider. 2008. Recruitment dynamics of lake trout in Western Lake Superior during 1988–1995. North American Journal of Fisheries Management 28(3):663-677.

Cox, S. P., and J. F. Kitchell. 2004. Lake Superior Ecosystem, 1929-1998: Simulating alternative hypotheses for recruitment failure of lake herring (*Coregonus artedi*). Bulletin of Marine Science 74(3):671-683.

Desorcie, T. J., and C. A. Bowen. 2003. Evidence of offshore lake trout reproduction in Lake Huron. North American Journal of Fisheries Management 23(4):1253-1256.

Dryer, W. R. 1964. Movements, growth, and rate of recapture of whitefish tagged in the Apostle Islands area of Lake Superior. U.S. Fish and Wildlife Service Fishery Bulletin 63:611-618.

Dryer, W. R. 1966. Bathymetric distribution of fish in the Apostle Islands region, Lake Superior. Transactions of the American Fisheries Society 95(3):248-259.

Dryer, W. and J. Beil. 1964. Life history of lake herring in Lake Superior. U.S. Fish and Wildlife Service Fishery Bulletin 63: 493-530.

Ebener, M. P. 1997. Recovery of lake whitefish populations in the Great Lakes: a story of successful management and just plain luck. Fisheries 22(7):18-20.

Ebener, M., editor. 2003. Sampling and reporting protocols for the Lake Superior Technical Committee. Lake Superior Technical Committee, Sault Ste. Marie, Michigan.

Ebener, M. P., and coauthors. 2008a. Management of lake whitefish commercial fisheries. Pages 99-143 *in* M. G. Schechter, N. J. Leonard, and W. W. Taylor, editors. International governance of fisheries ecosystems: Learning from the past, finding solutions for the future. American Fisheries Society, Bethesda, Md.

Ebener, M. P., and coauthors. 2008b. Status of cisco (*Coregonus artedi)* in Lake Superior during 1970-2006 and management and research considerations. A report of the Lake Superior Technical Committee to the Great Lakes Fishery Commission, Ann Arbor, MI.

Eschmeyer, P. H. 1955. The reproduction of lake trout in Southern Lake Superior. Transactions of the American Fisheries Society 84(1):47-74.

Eschmeyer, P. H., and A. M. Phillips. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. Transactions of the American Fisheries Society 94(1):62-74.

Eshenroder, R. L. and M. K Burnham-Curtis. 1999. Species succession and sustainability of the Great Lakes fish community. Pages 145-184 *in* W.W. Taylor and C.P. Ferreri, editors. Great Lakes fisheries policy and management. Michigan State University Press, East Lansing, MI.

ESRI. 2011. ArcGIS 10. Environmental Systems Research Institute (ESRI), Redlands, CA.

Fabrizio, M. C., R. M. Dorazio, and S. T. Schram. 2001. Dynamics of individual growth in a recovering population of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries & Aquatic Sciences 58(2):262.

Fabrizio, M. C., M. E. Holey, P. C. McKee, and M. L. Toneys. 1997. Survival rates of adult lake trout in Northwestern Lake Michigan, 1983–1993. North American Journal of Fisheries Management 17(2):413-428.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Sage, Thousand Oaks, CA.

Freeberg, M. H., W. W. Taylor, and R. W. Brown. 1990. Effect of egg and larval survival on year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. Transactions of the American Fisheries Society 119(1):92-100.

Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107(43):18286-18293.

Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution 18(9):448-455.

Gordon, S. 1954. The economic theory of a common-property resource: The fishery. The Journal of Political Economy 62(2):124-142.

Gorman, O. T. 2007. Changes in a population of exotic rainbow smelt in Lake Superior: Boom to bust, 1974-2005. Journal of Great Lakes Research 33(sp1):75-90.

Gorman, O. T., L. M. Evrard, G. A. Cholwek, J. M. Falck, and M. R. Vinson. 2010. Status and trends of prey fish populations in Lake Superior, 2009. Report presented to the Great Lakes Fishery Commission, Lake Superior Committee Meeting, Windsor, CA, March 23, 2010.

Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc., Sunderland, MA.

Gray, N. J. 2010. Sea change: Exploring the international effort to promote marine protected areas. Conservation & Society 8(4):331-338.

Great Lakes GIS. 2005. Great Lakes GIS, A geographic information system for Great Lakes Aquatic Habitat. Great Lakes GIS Project of the University of Michigan, Michigan Department of Natural Resources, Institute for Fisheries Research, Ann Arbor, MI. Available: http://ifrgis.snre.umich.edu/projects/GLGIS/

Guidetti, P., and F. Micheli. 2011. Ancient art serving marine conservation. Frontiers in Ecology and the Environment 9(7):374-375.

Halpern, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications 13(sp1):117-137.

Halpern, B. S., S. D. Gaines, and R. R. Warner. 2004. Confounding effects of the export of production and the displacement of fishing effort from marine reserves. Ecological Applications 14(4):1248-1256.

Halpern, B. S., S. E. Lester, and J. B. Kellner. 2010. Spillover from marine reserves and the replenishment of fished stocks. Environmental Conservation 36(4):268–276.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5(3):361-366.

Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:1871-1878.

Hansen, M. J., editor. 1996. A lake trout restoration plan for Lake Superior. Great Lakes Fishery Commission, Ann Arbor, MI.

Hansen, M. J. 1999. Lake trout in the Great Lakes: Basinwide stock collapse and binational restoration. Michigan State University Press, East Lansing.

Hansen, M. J., and coauthors. 1994. Declining survival of lake trout stocked during 1963–1986 in U.S. waters of Lake Superior. North American Journal of Fisheries Management 14(2):395-402.

Hansen, M. J., and coauthors. 1996. Causes of declining survival of lake trout stocked in U.S. waters of Lake Superior in 1963–1986. Transactions of the American Fisheries Society 125(6):831-843.

Hansen, M. J., and coauthors. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959-1993. Journal of Great Lakes Research 21(sp1):152-175.

Harvey, C. J., and J. F. Kitchell. 2000. A stable isotope evaluation of the structure and spatial heterogeneity of a Lake Superior food web. Canadian Journal of Fisheries and Aquatic Sciences 57(7):1395-1403.

Hedges, K. J., M. A. Koops, N. E. Mandrak, and O. E. Johannsson. 2010. Use of aquatic protected areas in the management of large lakes. Aquatic Ecosystem Health & Management 13(2):135-142.

Hedges, K. J., N. E. Mandrak, M. A. Koops, and O. E. Johannsson. 2011. Great Lakes aquatic protected areas. Non-Theme Area Research Report (White Paper) to the Great Lakes Fishery Commission, Ann Arbor, MI. Available: http://www.glfc.org/research/APA%20final%20white%20paper%202011.pdf

Hilborn, R., and coauthors. 2004. When can marine reserves improve fisheries management? Ocean & Coastal Management 47:197-205.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Routledge, Chapman and Hall, Inc.

Hoff , M. H., and O. T. Gorman. 2007. Prey fishes. Pages 43-48 *in* M.P. Ebener, editor. The state of Lake Superior in 2000. Great Lakes Fishery Commission Special Publication 07-02, pp. 43-48.

Holey, M. E., and coauthors. 1995. Progress toward lake trout restoration in Lake Michigan. Journal of Great Lakes Research 21(Supplement 1):128-151.

Hrabik, T. R., O. P. Jensen, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. Canadian Journal of Fisheries & Aquatic Sciences 63(10):2286-2295.

Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology & Evolution 20(7):380-386.

Jackson, J. B. C., and coauthors. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530):629-637.

Jacobs, G. R., C. P. Madenjian, D. B. Bunnell, and J. D. Holuszko. 2010. Diet of lake trout and burbot in Northern Lake Michigan during spring: Evidence of ecological interaction. Journal of Great Lakes Research 36(2):312-317.

Janssen, J., and coauthors. 2006. Evidence of lake trout reproduction at Lake Michigan's Mid-lake Reef Complex. Journal of Great Lakes Research 32(4):749-763.

Jensen, A. L. 1981. Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchell). Journal of Fish Biology 19(5):557-573.

Jensen, O. P., T. R. Hrabik, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. Canadian Journal of Fisheries & Aquatic Sciences 63(10):2296-2307.

Johnson, T. B., and coauthors. 2004. Spatial patterns in assemblage structures of pelagic forage fish and zooplankton in Western Lake Superior. Journal of Great Lakes Research 30(Supplement 1):395-406.

Jones, P. J. S. 1994. A review and analysis of the objectives of marine nature reserves. Ocean & Coastal Management 24(3):149-178.

Jones, P. J. S. 2002. Marine protected area strategies: issues, divergences and the search for middle ground. Reviews in Fish Biology and Fisheries 11(3):197-216.

Jones, P. J. S. 2006. Collective action problems posed by no-take zones. Marine Policy 30(2):143-156.

Kapuscinski, K. L., M. J. Hansen, and S. T. Schram. 2005. Movements of lake trout in U.S. waters of Lake Superior, 1973–2001. North American Journal of Fisheries Management 25(2):696-708.

Kelleher, G., and R. Kenchington. 1992. Guidelines for establishing marine protected areas. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

Kitchell, J. F., and coauthors. 2000. Sustainability of the Lake Superior fish community: Interactions in a food web context. Ecosystems 3(6):545-560.

Krueger, C. C., M. L. Jones, and W. W. Taylor. 1995. Restoration of lake trout in the Great Lakes: Challenges and strategies for future management. Journal of Great Lakes Research 21(sp1):547-558.

Krueger, C. C., B. L. Swanson, and J. H. Selgeby. 1986. Evaluation of hatchery-reared lake trout for reestablishment of populations in the Apostle Islands region of Lake Superior, 1960-84. Pages 93-107 *in* R. H. Stroud, editor. Fish culture in fisheries management. American Fisheries Society, Bethesda, MD.

Kutner, M. H., C. J. Nachtsheim, J. Neter, and W. Li. 2005. Applied linear statistical models, 5th edition. McGraw-Hill Irwin, New York, NY.

Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8(sp1):S72-S78.

Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior: Effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29(6):765-776.

Lawrie, A. H. and J. F. Rahrer. 1973. Lake Superior: A case history of the lake and its fisheries. Technical Report No. 19. Great Lakes Fishery Commission, Ann Arbor, MI. Available: http://www.glfc.org/pubs/TechReports/Tr19.pdf.

Le Quesne, W. J. F., and E. A. Codling. 2009. Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. ICES J. Mar. Sci. 66(1):122-131.

Linton, B. C., M. J. Hansen, S. T. Schram, and S. P. Sitar. 2007. Dynamics of a recovering lake trout population in Eastern Wisconsin waters of Lake Superior, 1980–2001. North American Journal of Fisheries Management 27(3):940-954.

Liu, J., and coauthors. 2007. Complexity of coupled human and natural systems. Science 317(5844):1513-1516.

Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: The emerging science of marine reserves. Ecological Applications 13(sp1):3-7.

Lynch, A. J., W. W. Taylor, and K. D. Smith. 2010. The influence of changing climate on the ecology and management of selected Laurentian Great Lakes fisheries. Journal of Fish Biology 77(8):1764-1782.

MacCallum, W. R., and J. H. Selgeby. 1987. Lake Superior revisited 1984. Canadian Journal of Fisheries and Aquatic Sciences 44(S2):s23-s36.

Madenjian, C. P., and T. J. DeSorcie. 1999. Status of lake trout rehabilitation in the Northern Refuge of Lake Michigan. North American Journal of Fisheries Management 19(3):658-669.

Madenjian, C. P., and T. J. Desorcie. 2010. Lake trout population dynamics in the Northern Refuge of Lake Michigan: Implications for future rehabilitation. North American Journal of Fisheries Management 30(3):629-641.

Madenjian, C. P., and coauthors. 2004. Status of lake trout rehabilitation on Six Fathom Bank and Yankee Reef in Lake Huron. North American Journal of Fisheries Management 24(3):1003-1016.

Madenjian, C. P., M. P. Ebener, and T. J. Desorcie. 2008. Lake trout population dynamics at Drummond Island Refuge in Lake Huron: Implications for future rehabilitation. North American Journal of Fisheries Management 28(4):979-992.

Maindonald, J. H., and J. Braun. 2007. Data analysis and graphics using R: An example-based approach, 2 edition. Cambridge University Press, New York, NY.

Marsden, J. E., and coauthors. 1995. Lake trout spawning habitat in the Great Lakes - a review of current knowledge. Journal of Great Lakes Research 21(sp1):487-497.

Maunder, M. N., and A. E. Punt. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research 70(2-3):141-159.

McKee, P. C., M. L. Toneys, M. J. Hansen, and M. E. Holey. 2004. Performance of two strains of lake trout stocked in the Midlake Refuge of Lake Michigan. North American Journal of Fisheries Management 24(4):1101-1111.

MDNR. 2011. 2011 Michigan fishing guide. Michgian Department of Natural Resources. Available: http://www.michigan.gov/documents/dnr/FishingGuide_11-low-res_347106_7.pdf. (October 13, 2011).

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications 14(6):1709-1723.

Myers, J. T., M. L. Jones, J. D. Stockwell, and D. L. Yule. 2009. Reassessment of the predatory effects of rainbow smelt on ciscoes in Lake Superior. Transactions of the American Fisheries Society 138(6):1352-1368.

National MPA Center. 2008. Framework for the National System Of Marine Protected Areas of the United States Of America. National Oceanic and Atmospheric Administration and Department of the Interior, Silver Spring, MD. Available: http://mpa.gov/pdf/national-system/finalframework_full.pdf

Nelson, M. P. 1998. An amalgamation of wilderness preservation arguments. Pages 154-198 *in* J. B. Callicot, and M. P. Nelson, editors. The great new wilderness debate. University of Georgia Press, Athens, GA.

Nelson, M. P. 2005. The great new wilderness debate: An overview. Pages 200-208 *in* L. P. Pojman, editor. Environmental ethics: Readings in theory and application, 4th edition. Wadsworth, Belmont, CA.

Nieland, J. L., M. J. Hansen, M. J. Seider, and J. J. Deroba. 2008. Modeling the sustainability of lake trout fisheries in eastern Wisconsin waters of Lake Superior. Fisheries Research 94(3):304-314.

NOAA. 2011a. Marine Protected Areas Inventory. National Marine Protected Areas Center. Available: http://www.mpa.gov/dataanalysis/mpainventory/. (October 4, 2011).

NOAA. 2011b. Snapshot of Great Lakes MPAs. Analysis of U.S. MPAs. National Marine Protected Areas Center, Data and Analysis. Available: http://www.mpa.gov/pdf/helpful-resources/greatlakes_mpa_snapshot.pdf. (October 4, 2011).

Nowlis, J. S., and A. Friedlander. 2004. Research priorities and techniques. Pages 128-163 *in* J. Sobel and C. Dahlgren, editors. Marine Reserves: A guide to science, design, and use. Island Press, Washington, D.C.

NRC (National Research Council). 2001. Marine Protected Areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C.

Pajaro, M. G., M. E. Mulrennan, J. Alder, and A. C. J. Vincent. 2010. Developing MPA effectiveness indicators: Comparison within and across stakeholder groups and communities. Coastal Management 38(2):122 - 143.

Pauly, D., and coauthors. 2002. Towards sustainability in world fisheries. Nature 418(6898):689-695.

Pelc, R. A., R. R. Warner, S. D. Gaines, and C. B. Paris. 2010. Detecting larval export from marine reserves. Proceedings of the National Academy of Sciences 107(43):18266-18271.

Pelletier, D., J. Claudet, J. Ferraris, L. Benedetti-Cecchi, and J. A. Garcìa-Charton. 2008. Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. Canadian Journal of Fisheries & Aquatic Sciences 65(4):765-779.

Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. BioScience 35(11):707-717.

Pinnegar, J. K., and coauthors. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation 27(02):179-200.

Pollnac, R., and coauthors. 2010. Marine reserves as linked social–ecological systems. Proceedings of the National Academy of Sciences 107:18262–18265.

Pollock, K. H., J. Yoshizaki, M. C. Fabrizio, and S. T. Schram. 2007. Factors affecting survival rates of a recovering lake trout population estimated by mark–recapture in Lake Superior, 1969–1996. Transactions of the American Fisheries Society 136(1):185-194.

Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of Southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950-1970., Ann Arbor, MI.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York, NY.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahrer, J. F. 1968. Movements of adult lake trout in Lake Superior. Transactions of the American Fisheries Society 97(4):481-484.

Ray, B. A., and coauthors. 2007. Diet and prey selection by Lake Superior lake trout during Spring, 1986-2001. Journal of Great Lakes Research 33(1):104-113.

Reid, D. M., D. M. Anderson, and B. A. Henderson. 2001. Restoration of lake trout in Parry Sound, Lake Huron. North American Journal of Fisheries Management 21(1):156-169.

Roberts, C. M. 2003. Our shifting perspectives on the oceans. Oryx 37(02):166-177.

Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294(5548):1920-1923.

Roberts, C. M., J. P. Hawkins, and F. R. Gell. 2005. The role of marine reserves in achieving sustainable fisheries. Philosophical Transactions of the Royal Society B: Biological Sciences 360(1453):123-132.

Roseman, E. F., W. Stott, T. P. O'Brien, S. C. Riley, and J. S. Schaeffer. 2009. Heritage strain and diet of wild young of year and yearling lake trout in the main basin of Lake Huron. Journal of Great Lakes Research 35(4):620-626.

Russ, G. R., and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series 132:1-9.

Russ, G. R., and A. C. Alcala. 2003. Marine reserves: Rates and patterns of recovery and decline of predatory fish, 1983-2000. Ecological Applications 13(6):1553-1565.

Sale, P. F., and coauthors. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology & Evolution 20(2):74-80.

Sánchez Lizaso, J. L., and coauthors. 2000. Density dependence in marine protected populations: a review. Environmental Conservation 27(2):144-158.

Sanchirico, J. N., K. A. Cochran, and P. M. Emerson. 2002. Marine protected areas: Economic and social implications. Discussion Paper 02–26. Resources for the Future, Washington, D.C. Available: http://www.rff.org/documents/RFF-DP-02-26.pdf

Schram, S. T., T. B. Johnson, and M. J. Seider. 2006. Burbot consumption and relative abundance in the Apostle Islands region of Lake Superior. Journal of Great Lakes Research 32(4):798-805.

Schram, S. T., J. H. Selgeby, C. R. Bronte, and B. L. Swanson. 1995. Population recovery and natural recruitment of lake trout at Gull Island Shoal, Lake Superior, 1964-1992. Journal of Great Lakes Research 21(Supplement 1):225-232.

Seider, M. 2010a. 2009 Spring Lake Trout Assessment Report [Lake Superior]. Wisconsin Department of Natural Resources, Bayfield, WI.

Seider, M. 2010b. 2009 Summer Index Report [Lake Superior]. Wisconsin Department of Natural Resources, Bayfield, WI.

Seider, M. J., and S. T. Schram. 2011. Population dynamics of lake whitefish in the Apostle Islands region of Lake Superior. Wisconsin Department of Natural Resources, Bayfield, WI.

Selgeby, J. H. 1982. Decline of lake herring (*Coregonus artedii*) in Lake Superior: An analysis of the Wisconsin herring fishery, 1936–78. Canadian Journal of Fisheries and Aquatic Sciences 39(4):554-563.

Shipp, R. L. 2003. A perspective on marine reserves as a fishery management tool. Fisheries 28(12):10-21.

Sloan, N. A. 2002. History and application of the wilderness concept in marine conservation. Conservation Biology 16(2):294-305.

Sobel, J., and C. Dahlgren. 2004. Marine reserves: A guide to science, design, and use. Island Press, Washington, D.C.

Soto, C. G. 2001. The potential impacts of global climate change on marine protected areas. Reviews in Fish Biology and Fisheries 11(3):181-195.

Stanley, J. G., R. L. Eschenroder, and W. L. Hartman. 1987. Sanctuaries for lake trout in the Great Lakes. Contribution 676 of the National Fisheries Center - Great Lakes. Coastal Zone '87, Seattle, WA.

Stewart-Oaten, A., and J. R. Bence. 2001. Temporal and spatial variation in environmental impact assessment. Ecological Monographs 71(2):305-339.

Stewart-Oaten, A., J. R. Bence, and C. W. Osenberg. 1992. Assessing effects of unreplicated perturbations: No simple solutions. Ecology 73(4):1396-1404.

Stockwell, J. D., and coauthors. 2009. A synthesis of cisco recovery in Lake Superior: Implications for native fish rehabilitation in the Laurentian Great Lakes. North American Journal of Fisheries Management 29(3):626-652.

Stockwell, J. D., D. L. Yule, O. T. Gorman, E. J. Isaac, and S. A. Moore. 2006. Evaluation of bottom trawls as compared to acoustics to assess adult lake herring (*Coregonus artedi*) Abundance in Lake Superior. Journal of Great Lakes Research 32(2):280-292.

Swanson, B. L., and D. V. Swedberg. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*) predation. Canadian Journal of Fisheries and Aquatic Sciences 37(11):2074-2080.

Taylor, W. W., A. J. Lynch, and M. G. Schechter, editors. 2011. Sustainable fisheries: Multi-level approaches to a global problem. American Fisheries Society, Bethesda, MD.

Taylor, W. W., M. A. Smale, and M. H. Freeberg. 1987. Biotic and abiotic determinants of lake whitefish (*Coregonus ciupeaformis*) recruitment in Northeastern Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 44(sp2):s313-s323.

Vandeperre, F., and coauthors. 2010. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish and Fisheries 12:412–426.

Venables, W. N., and C. M. Dichmont. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70:319-337.

Watson, Alder, and Walters. 2000. A dynamic mass-balance model for marine protected areas. Fish and Fisheries 1(1):94-98.

WDNR. 2008. DNR Coordinate Reference System. http://dnr.wi.gov/maps/gis/wtm8391.html (June 2010).

WDNR. 2011. Guide to Wisconsin hook and line fishing regulations, 2011-2012. Wisconsin Department of Natural Resources, Bureau of Fisheries Management. Available: http://dnr.wi.gov/fish/regulations/2011/documents/FishingRegs11-12.pdf. (October 13, 2011).

WDNR, Bad River, and Red Cliff Bands of Lake Superior Tribe of Chippewa Indians. 2005. 2005 State-Tribal Lake Superior Agreement.

Willis, T. J., R. B. Millar, and R. C. Babcock. 2003a. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (*Sparidae*) in northern New Zealand marine reserves. Journal of Applied Ecology 40(2):214-227.

Willis, T. J., R. B. Millar, R. C. Babcock, and N. Tolimieri. 2003b. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation 30(02):97-103.

Wisconsin State Administrative Code. 2010. Fish refuges. NR 26.23 (October 2010). Available: https://docs.legis.wisconsin.gov/code/admin_code/nr/26/23?view=section.

Wisconsin State-Tribal Technical Committee. 2009. Recommended maximum lake trout harvest for the Apostle Islands region of Lake Superior for the 2010-2012 fishing years.

Worm, B., and coauthors. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314(5800):787-790.

Worm, B., and coauthors. 2009. Rebuilding global fisheries. Science 325(5940):578-585.

Yamamura, K. 1999. Transformation using $(x + 0.5)$ to stabilize the variance of populations. Researches on Population Ecology 41(3):229-234.

Yule, D. L., and coauthors. 2006. Evaluation of methods to estimate lake herring spawner abundance in Lake Superior. Transactions of the American Fisheries Society 135(3):680-694.

Yule, D. L. S., Jason D., J. A. Black, K. I. Cullis, G. A. Cholwek, and J. T. Myers. 2008. How systematic age underestimation can impede understanding of fish population dynamics: Lessons learned from a Lake Superior cisco stock. Transactions of the American Fisheries Society 137(2):481-495.