Effectiveness of the Gull Island Refuge for Lake Trout in Lake Superior

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Melissa J. Johnson

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APPROVED BY THE GRADUATE COMMITTEE OF:

Dr. Kevin R. Russell, Committee Chairman
Associate Professor of Wildlife Ecology
College of Natural Resources

Dr. Michael J. Hansen
Research Fishery Biologist, Field Station Supervisor
USGS-Great Lakes Science Center

Dr. Dan Isermann
Assistant Professor of Fisheries and Water Resources
College of Natural Resources

Dr. Jason Riddle
Assistant Professor of Wildlife Ecology
College of Natural Resources

Michael J. Seider
Fishery Biologist
US Fish and Wildlife Conservation Office

Abstract

The Gull Island refuge was created in 1976 in response to overfishing of the lake trout population in the Apostle Islands. My objective was to determine if lake trout abundance, growth, maturity, and mortality differed inside and outside the refuge, before and after the refuge was created. To address my objective, I compared abundance, growth, maturity, and mortality between lake trout captured inside and outside the refuge during spring large-mesh and summer graded-mesh gill-net surveys. Wild adult lake trout abundance increased significantly, while stocked adult lake trout abundance decreased significantly after the refuge was created. Wild adult and juvenile lake trout were significantly more abundant inside than outside the refuge, and stocked adult lake trout were less abundant inside than outside the refuge. Lake trout grew faster to a shorter asymptotic length inside the refuge than outside the refuge. Lake trout matured at an older age inside the refuge than outside the refuge. Lake trout suffered significantly lower mortality inside the refuge than outside the refuge. I conclude that the Gull Island refuge enhanced wild lake trout population growth in the Apostle Islands region and should be retained in the future to sustain conditions that favor population growth.

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Introduction

Aquatic Protected Areas (APAs) are important tools for managing fisheries that can complement and strengthen traditional fisheries management (Carr and Reed 1993; Russ and Alcala 1996; Agardy 2000; Murawski et al. 2004). The definition of an APA has several different meanings, the most direct being defined as a geographic area with discrete boundaries that has been designated to enhance conservation of marine [aquatic] resources (Lydecker, 2004). The International Union of Conservation of Nature (IUCN) defined an APA "as any area of inter-tidal or sub-tidal terrain, together with its overlying water and associated flora, fauna, historical, or cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (Agardy et al. 2003). An APA can facilitate recuperation of an exploited stock by preserving genetic diversity, maintaining population size and age structure, and providing recruitment outside the refuge, often referred to as "spillover" (Carr and Reed 1993; Man et al. 1995; Russ and Alcala 1996; Halpern 2003; Halpern and Warner 2003; Murawski et al. 2004). For fish, increased genetic diversity, large population size, protection of spawning biomass, reduction of overfishing, and increased age diversity are effects of retaining older, larger individuals and increasing recruitment of younger, smaller individuals (Carr and Reed 1993; Man et al. 1995; Lauck et al. 1998; Agardy 2000).

In general, APAs are associated with increases in marine organism size, biomass, density, and diversity. For example, APAs in St. Lucia and Chile were both associated with significantly larger biomass and organism size inside than outside reserves (Halpern 2003). Biomass nearly tripled, organism size increased 20−30%, and density doubled inside compared to outside, for 81 different APAs across the world, although such differences cannot predict how any particular organism may react to an APA (Halpern 2003). APAs can also buffer against declines in abundance while hastening recovery by supplying greater egg output, adding new recruits to a harvestable population, protecting spawning adults, maintaining depletion-prone species, and providing undisturbed spawning and nursery habitat (Carr and Reed 1993; Man et al. 1995; Russ and Alcala 1996; Agardy 2000). Further, an APA is often viewed as an economic benefit because of the potential increase in recreational fishing revenue through spillover into the surrounding area (Carr and Reed 1993; Agardy 2000). Spillover occurs when adults leave the nursery and spawning area to forage outside an APA, which can increase fish yield in the area around an APA while creating a buffer that protects fish within the APA (Carr and Reed 1993; Russ and Alcala 1996; Agardy 2000; Halpern and Warner 2003; Roberts et al. 2005).

APAs have limitations and problems that persist after establishment of boundaries. APAs are predicted to lead to trophic cascade effects by protecting predators from fishing, thereby increasing predator abundance while decreasing prey abundance (Halpern 2003). Open-water systems, such as banks and estuaries, are dynamic complexes, so living organisms move in space according to physical, mainly nondeterministic, patterns. Highly mobile species can move in and out of human-implemented boundaries to be vulnerable to harvest (Allison et al. 1998; Agardy 2000). Spillover may inadvertently increase fishing pressure around the APA, instead of displacing fishing pressure around the border, and thereby reduce peripheral fish populations and prevent reproductive adults from entering the refuge for spawning (Allison et al. 1998; Roberts et al. 2005). Although fishing pressure can be displaced, this hardly necessitates abandoning APAs that are used in conjunction with other fisheries management regulations, and reinforces the idea that APAs should be placed in areas with known vulnerability, such as spawning habitat (Roberts et al. 2005).

Past fishing pressure in the Laurentian Great Lakes created a need for better fisheries management. Commercial fishing in the Great Lakes grew intensively beginning in the late 1800s (Hansen 1999; Nieland et al. 2008). The commercial fishery targeted several species, most notably the lake trout (*Salvelinus namaycush*), an apex predator that was economically valuable to fisheries (Bronte et al. 1995; Nieland et al. 2008). Lake trout populations collapsed in the Great Lakes, in Ontario in the 1930s and 1940s, Huron in 1935, Michigan in 1943, and Superior after 1960 (Pycha and King 1975; Linton et al. 2007; Nieland et al. 2008). By 1962, lake trout were nearly extirpated from all the Great Lakes. Advances in commercial fishing such as development of steam tug boats (and later motor boats), multifilament and monofilament gill-net line, and the hydraulic gill-net lifter contributed to the collapse (Hansen 1999; Nieland et al. 2008). Commercial lake trout fisheries shifted gill-net effort from one lake to another and from across the lake to new populations to pursue remnant stocks, a process known as 'fishing up' (Nieland et al. 2008). Harvest statistics were first available in 1879 when annual harvest of lake trout was less than 1-million kg and peaked at 3-million kg in 1903 (Hile et al. 1951; Baldwin et al. 1979). Between 1913 and 1950, Lake Superior supported an average of 2-million kg of annual lake trout harvest (Lawrie and Rahrer 1973; Baldwin et al. 1979; Hansen 1996; Linton et al. 2007). A consistent yield of 2-million kg annually suggested a sustainable yield during this period, but in Michigan waters during the 1940s, yield was maintained by increasing fishing intensity and gill-net efficiency, despite a

50% decline in abundance (Hile et al. 1951; Pycha and King 1975; Swanson and Swedberg 1980; Linton et al. 2007; Corradin et al. 2008). This form of fishing intensity proved fatal to a species that is long-lived, slow growing, and late maturing (Russ and Alcala 1996; Agardy 2000; Corradin et al. 2008), where 50% of females in Lake Superior do not reach maturity until age eight (Nieland et al. 2008).

Sea lamprey began colonizing the Great Lakes towards the end of lake trout fishery collapses in each lake, further accelerating extirpation of the species during 1953–1961 in Lake Superior (Pycha and King 1975; Swanson and Swedberg 1980). In Wisconsin waters of Lake Superior, spawning female lake trout were conspicuously absent from spawning grounds at Gull Island Shoal (Swanson and Swedberg 1980; Bronte et al. 1995; Hansen et al. 1995; Schram et al. 1995). In response, research on lake trout recovery intensified. The Lake Superior Technical Committee aimed to increase recruitment by stocking hatchery-origin fish, reduce mortality by fishery regulations, and suppress the sea lamprey by use of chemicals and barriers (Lawrie and Rahrer 1973; Swanson and Swedberg 1980; Hansen et al. 1995; Linton et al. 2007). Starting in 1963, lake trout were consistently stocked although survival of hatchery lake trout declined in Wisconsin waters in the 1970s and 1980s (Hansen et al. 1994; Linton et al. 2007). This decline was attributed to various factors including commercial fishing effort (Hansen et al. 1996). However, early reports revealed that stocked fish fueled recovery while wild fish contributed little between 1959 and 1993 in Wisconsin waters of Lake Superior (Lawrie and Rahrer 1973; Hansen et al. 1995). Nevertheless, wild lake trout abundance was the main source of recruitment at Gull Island Shoal, a historically important offshore spawning reef in Wisconsin waters, during that period (Schram et al. 1995). Wild lake trout density increased while stocked density decreased in western Lake Superior during 1980–2003 (Corradin et al. 2008).

Recovery of the wild lake trout population would not likely have occurred without further protection by the state. During 1962–1970, lake trout commercial fishing was prohibited in Wisconsin waters and the Gull Island Shoal population was lightly exploited only by fishing for assessment purposes (Schram et al. 1995). Subsequently, fishing effort increased dramatically with a growing lake trout population. Though intensive stocking and sea lamprey control were underway, lake trout were still treated as by-catch and inconsistencies in fishing regulations among jurisdictions resulted in commercial fishing returning to excessive levels in the 1970s (Pycha and King 1975; Nieland et al. 2008). By 1975, overfishing caused the population to decline once more, which prompted the State of Wisconsin to establish two year-round, harvest-free zones, Gull Island Shoal (GIS) refuge in 1976 and Devils Island Shoal (DIS) refuge in 1981 (Figure 1; Swanson and Swedberg 1980; Schram et al. 1995; Nieland et al. 2008). Gull Island Shoal is a historically important spawning area that has been a source of recruitment to the lake trout population in surrounding waters (Bronte et al. 1995). Increased abundance of wild females after 1976 and increased recruitment after 1977 was attributed to the refuge (Schram et al. 1995). Lake trout tagged in the refuge during autumn are recaptured outside the refuge, thereby suggesting refuge boundaries did not encompass the entire range of lake trout spawning on Gull Island Shoal (Rahrer 1968; Schram et al. 1995; Kapuscinski et al. 2005). Although previous studies have suggested the GIS refuge played an important role in lake trout rehabilitation in the Apostle Islands, no study has specifically examined its impact on population characteristics.

My objective was to determine if lake trout population characteristics differed inside and outside the Gull Island refuge, before and after the refuge was implemented in 1976. I compared abundance of lake trout residing inside and outside the refuge during the period of stock collapse and recovery. I indexed abundance as geometric-mean catch/net-night of lake trout caught during spring large-mesh and summer graded-mesh gill-net surveys. I then compared growth, maturity, and mortality inside and outside the refuge in four periods during 1981–2010 that corresponded to four generations of lake trout, the first of which was hatched before the refuge was established. For growth, I used a nonlinear length-age model to estimate asymptotic length and growth rate. For maturity, I used a logistic model to estimate length and age at 50% maturity. For mortality, I used a catch-curve model to estimate the instantaneous total mortality rate. I expected to find higher lake trout abundance inside the refuge than outside the refuge, with fish growing slower, maturing at an older age, and suffering lower mortality inside the refuge than outside the refuge.

Methods

Study Site

Gull Island Shoal (46°57′N, 90°24′W) is located in western Lake Superior, within the Apostle Islands (Figure 1). The Apostle Islands encompass 22 islands and 447,337 ha of lake surface area. Water depths are relatively shallow and seldom exceed 65 m, except for a 140-m trench near the eastern boundary of the islands. The refuge includes a shoal for which it is named, Gull and Michigan islands (46°54′N, 90°27′W), and a 70,000-ha nursery area (46°52′N, 90°28′W) near the eastern edge of the Apostle Islands (Figure 1). Gull Island Shoal encompasses nearly 3,100 ha of rocky substrate in 1−20 m of water and is surrounded by water deeper than 70 m. Lake trout aggregate on the shoal in October each year. Nursery habitat depth ranges from 10 m near Michigan Island to 40 m farther from shore, surrounded by 70-m deep water. Nursery habitat is sand substrate with a few isolated rock ridges (Bronte et al. 1995; Schram et al. 1995). Age-0 lake trout move from spawning habitat on Gull Island Shoal to the Michigan Island nursery area (Bronte et al. 1995). Although deemed a no-harvest refuge seasonal and depth restricted fishing opportunities exist within the GIS refuge. Commercial fishing is allowed in waters deeper than 64 m, tribal gill-net fishing is seasonally open from November 5 to December 6 at a depth of 7 fathoms (12.8 m) and commercial fishing for herring with float nets is allowed at depths shallower than 25 fathoms (45.7 m; WDNR 2011).

Field Sampling

Lake trout have been the target of intensive studies since the early 1950s through fishery-independent index netting by the WDNR in Bayfield, Wisconsin. Fixed stations or areas were sampled annually with multifilament or monofilament gill nets throughout the Apostle Islands region each year (Figure 1). Adult lake trout were sampled during annual spring large-mesh gill-net surveys from 1959 to 2010. Adult and juvenile lake trout were captured in summer graded-mesh gill-net surveys from 1970 to 2010. Spawning adult lake trout were sampled during autumn large-mesh gill-net surveys from 1951 to 2010. Lake trout were tagged during each survey and recaptured later during WDNR surveys, commercial netting fisheries, and recreational angling fisheries.

Spring large-mesh surveys

The large mesh survey was done in April through early June in most years by contracted commercial fishers from 1959 to 1980 and WDNR from 1981 to 2010 (except in 1996 and 2001). Each bottom-set gill-net was 823-m long with a 114-mm stretched-mesh, 210/2 multifilament-nylon twine, 18 meshes deep, and hung on the ½ basis. Each net gang was soaked for an average of three nights prior to 2001 and one night after 2001.

Summer graded-mesh surveys

Fixed stations were sampled with bottom-set gill-nets in July and August from 1970 to 1979, and in even-numbered years from 1980 to 2010, except for 1996. Gill-nets were 1,092-m long and set for 24 hours at depths of 4–115 m. All nets contained twelve 91-m panels of different stretch meshes from 38 to 178 mm in 12.7-mm increments. Multifilament and monofilament nylon gill-nets were used until 1989 and monofilament nets were used exclusively thereafter.

Biological Data

During each survey, total length, weight of dead fish, tag type, colour, and number, fin clips, sea lamprey wound presence, sex, and maturity status (for dead fish, or through expression of milt or eggs, in autumn samples only) were recorded. Lake trout were selected randomly from each sample or based on filling length bins. Sagittal otoliths and scales from dead lake trout were removed to estimate age.

Data Analysis

Relative abundance of lake trout during the period of stock collapse and recovery was compared before and after establishment of the refuge in 1976. Abundance, growth, maturity, and mortality were compared for lake trout captured inside and outside the refuge during the period of stock collapse and recovery.

Relative Abundance

Relative abundance (CPE = catch per effort) of lake trout was described as the number of fish caught per 1000 m of net. For spring large-mesh surveys, lake trout CPE was estimated as CPE per station for each year using the net saturation model adjusted for variability in soak time (± 95% confidence limits):

$$(1) \qquad Adjusted\ CPE = \alpha\ (1 - e^{-\beta \times NIGHTS})$$

$$(2) \qquad \beta = \frac{-log_e(1-\frac{CPE}{211.443})}{NIGHTS}$$

In equation (1), α is the maximum CPE that would be attained from a fully saturated net (211.443), β is the rate at which CPE approaches α (equation (2), and nights is the time between setting and lifting (Hansen et al. 1998). Geometric mean CPE across all stations was calculated for each year.

For summer graded-mesh surveys, lake trout CPE was defined as the number of fish caught per 1,000 m of net:

$$(3) \qquad CPE = Log\left(\left(\frac{Total(CATCH)}{[(GANG\ LENGTH \times NIGHTS) \times 1000]}\right) + 1\right)$$

In equation (3), CPE is the logarithm of total catch over gang length and nights, where nights represent time between setting and lifting. Geometric mean CPE across all stations was calculated for each year.

Lake trout abundance was compared inside and outside the refuge using 2-way ANOVA of the survey stations sampled during and after stock collapse. The difference between lake trout CPE inside and outside the refuge was judged significant if $P \leq 0.05$. Spring large-mesh lake trout survey CPE from 1959 to 2010 and summer graded-mesh lake trout survey CPE from 1976 to 2010 were used to evaluate refuge effects because spawning adult abundance is insensitive to abundance changes caused by aggregation of adults on spawning habitat.

Growth

Lake trout captured in spring large-mesh and summer graded-mesh surveys during 1981–2010 were used for analysis of growth. Growth was quantified using the Von Bertalanffy length-age model:

$$(4) \qquad L_t = L_\infty(1 - e^{-K(t-t_0)})e^{\varepsilon}$$

In equation (4), L_t is the mean length at age of capture (t), L_∞ is average asymptotic length, K is the instantaneous rate at which L_t approaches L_∞, t_0 is the theoretical age at zero length, and ε is multiplicative process error. Nonlinear regression was used to estimate model parameters, L_∞, K, and t_0, and their asymptotic standard errors (Seber and Wild 1989). A likelihood-ratio test ($P \leq 0.05$) was used to compare growth models between fish captured inside and outside the refuge during four periods corresponding to four generations of lake trout, including the last generation hatched before the refuge was instituted (1981−1984) and three generations protected by the refuge (1985−1992, 1993−2000, and 2001−2010).

Maturity

Lake trout captured in spring large-mesh and summer graded-mesh surveys during 2001–2010 were used for analysis of maturity. Maturity was estimated using a logistic regression model based on the maturity status of individual lake trout sampled in each length or age class:

$$(5) \qquad M = \frac{1}{(1+e^{-(b_0-b_1X)})}$$

In equation (5), M is the maturity status of individual lake trout (1 = sexually mature; 2 = sexually immature) at length or age X, and b_0 and b_1 describe the rate of increase in the probability of maturity with increasing length or age. Model parameters, b_0 and b_1, and their standard errors were estimated using logistic regression. Length and age at 50% maturity, $X_{0.5}$, was estimated as the ratio of the absolute value of the intercept, $|b_0|$, to the slope, b_1. A likelihood-ratio test ($P \leq 0.05$) was used to compare maturity between lake trout residing inside and outside the refuge during 2001–2010, because maturity was not assessed in earlier periods.

Mortality (Survival)

Lake trout captured in spring large-mesh and summer graded-mesh surveys during 1981–2010 were used for analysis of mortality. Mortality was estimated using catch-curve regression of the number of each age class of lake trout captured:

(6) $$N_t = N_0 e^{-Zt} e^{\varepsilon}$$

(7) $$log_e(N_t) = log_e(N_0) - Zt + \varepsilon$$

(8) $$log_e(N_t) = log_e(N_0) - Zt + b_1 X + b_2(X \times t) + \varepsilon$$

In equation (6), N_t is the number captured at age *t*, N_0 is the average number of age-0 recruits that gave rise to age-classes represented in the age frequency of the catch curve, and *Z* is the instantaneous total mortality rate. Model parameters, N_0 and *Z*, and their standard errors were estimated using linear regression of the $\log_e$-transformed equation (7). Mortality was compared between lake trout captured inside and outside the refuge within the same four periods in which growth was compared (1981−1984, 1985−1992, 1993−2000, and 2001−2010) using ANCOVA, equation (8), in which the interaction between age *t* and length or age *X* tests homogeneity of total instantaneous mortality *Z* ($P \leq 0.05$; Sokal and Rohlf 1981). Annual survival *S* and mortality *A* were estimated from total instantaneous mortality *Z* as $S = e^{-Z}$ and $A = 1 - S$.

Results

Relative Abundance

Based on spring large-mesh gill-netting, total lake trout abundance did not change significantly during 1959–2010, because stocked lake trout abundance decreased while wild lake trout abundance increased in the Apostle Islands region of Lake Superior. Total abundance of stocked and wild lake trout did not change significantly ($F_{1, 48}$ = 3.904; P = 0.054), because abundance of stocked lake trout declined significantly ($F_{1, 48}$ = 10.632; P = 0.002) while abundance of wild lake trout increased significantly ($F_{1, 48}$ = 31.445; P < 0.001; Figure 2). From 1970 through 2010, stocked lake trout abundance declined 99% while wild lake trout abundance increased steadily. Stocked lake trout were more abundant than wild lake trout from 1963 through 1986, whereas wild lake trout were more abundant than stocked lake trout before 1963 and after 1986.

Based on spring large-mesh gill-netting, wild lake trout increased and were more abundant inside than outside the refuge, whereas stocked lake trout decreased and were more abundant outside than inside the refuge in the Apostle Islands region of Lake Superior during 1976−2010. Wild lake trout were significantly more abundant inside the refuge than outside the refuge ($F_{1, 64}$= 41.36; $P \leq 0.001$), whereas stocked lake trout were significantly less abundant inside the refuge than outside the refuge ($F_{1, 64}$= 6.91; P = 0.011; Figure 3). Wild lake trout abundance began to increase prior to 1985, whereas stocked lake trout abundance began to decrease after 1986 inside and outside the refuge.

Based on summer graded-mesh gill-netting, wild lake trout increased and were more abundant inside than outside the refuge, whereas stocked lake trout decreased but did not differ in abundance inside and outside the refuge in the Apostle Islands region of

Lake Superior during 1976−2010. Wild lake trout abundance was significantly greater inside than outside the refuge ($F_{1, 36}$= 28.009; $P \leq 0.001$), whereas stocked lake trout abundance did not differ significantly inside and outside the refuge ($F_{1, 36}$= 0.461; P = 0.501; Figure 4). Abundance of wild lake trout increased more rapidly inside the refuge than outside the refuge, whereas abundance of stocked lake trout decreased at a similar rate inside and outside the refuge.

Growth

Lake trout grew similarly inside and outside the Gull Island refuge before 2001, whereas those outside the refuge grew faster than those inside the refuge after 2000 in the Apostle Islands region of Lake Superior during 1981−2010. Lake trout grew similarly inside and outside the refuge during 1981–1984 ($F_{3, 11}$ = 3.315; P = 0.0608), 1985–1992 ($F_{3, 25}$ = 3.010; P = 0.0491), and 1993–2000 ($F_{3, 25}$ = 2.276; P = 0.0986; Table 1; Figure 5). In contrast, lake trout grew slower to a shorter asymptotic length inside the refuge than outside the refuge during 2001–2010 ($F_{3, 43}$ = 5.216; P = 0.0037; Table 1; Figure 5). Annual growth decreased at similar rates inside the refuge (from 7.3 in/year in 1981–1984 to 4.6 in/year in 2001–2010) and outside the refuge (from 2.1 in/year in 1981–1984 to 3.6 in/year in 2001–2010) during 1981–2010 (Table 1; Figure 6).

Maturity

Lake trout matured at a similar length but older age inside than outside the Gull Island refuge in the Apostle Islands region of Lake Superior during 2001−2010. Lake trout matured at a similar length inside the refuge ($L_{0.5}$ = 22.2 in) and outside the refuge ($L_{0.5}$ = 21.9 in) during 2001–2010 (Length×Refuge interaction; t = 0.745; P = 0.690; Table 2; Figure 7). In contrast, lake trout matured at a significantly older age inside the refuge ($A_{0.5}$ = 9.9 yr) than outside the refuge ($A_{0.5}$ = 8.8 yr) during 2001–2010 (Age×Refuge interaction; t = 2.496; P = 0. 0.0125; Table 2; Figure 7).

Mortality (Survival)

Lake trout survived similarly inside and outside the Gull Island refuge before 1993, whereas those inside the refuge survived better than those outside the refuge after 1992 in the Apostle Islands region of Lake Superior during 1981−2010. Lake trout sampled inside the refuge suffered similar mortality inside and outside the refuge during 1981–1984 ($F_{1, 10}$= 0.279; P = 0.609) and 1985–1992 ($F_{1, 20}$= 0.421; P = 0.524; Table 3; Figure 8). In contrast, lake trout sampled inside the refuge suffered significantly lower mortality than those sampled outside the refuge during both 1993–2000 ($F_{1, 28}$= 17.082; $P \leq 0.001$) and 2001–2010 ($F_{1, 26}$= 35.021; $P \leq 0.001$; Table 3; Figure 8). Annual survival increased faster inside the refuge (from 48.6% in 1981–1984 to 78.4% in 2001–2010) than outside the refuge (from 45.6% in 1981–1984 to 67.7% in 2001–2010 outside the refuge) during 1981–2010 (Table 3; Figure 6).

Discussion

I found that the Gull Island refuge encouraged growth of the lake trout population in Wisconsin waters of Lake Superior, like other protected areas that protect spawning and nursery grounds (Agardy 2000; Roberts et al. 2005). The refuge provided suitable habitat to encourage population growth in the Apostle Islands region (Bronte et al. 1995; Bronte et al. 2002), similar to 69 no-take refuges in St. Lucia and Chile, within which carnivorous, herbivorous, invertebrate, and planktivore species' density all significantly increased (Halpern 2003). I found that wild lake trout were more abundant inside the refuge, likely because of the importance of the refuge for spawning (Swanson and Swedberg 1980; Schram et al. 1995). Wild lake trout are assumed to exhibit natal homing (Swanson 1973). In contrast, I found that stocked lake trout were consistently less abundant inside the refuge, likely because they did not home to offshore spawning reefs in Wisconsin waters of Lake Superior (Swanson 1973), and instead, spawned in near-shore areas not formerly used by wild lake trout (Bronte et al. 2002). Stocked lake trout likely preferred to spawn inshore near stocking sites (Hansen 1995; Bronte et al. 2002). Recruitment of stocked lake trout progeny to refuge nursery grounds from inshore sites is unlikely because deep channels separated offshore shoals from inshore areas where stocked lake trout resided (Bronte et al. 1995). Further, I found that lake trout juveniles and adults were more abundant inside than outside the refuge, likely because they were progeny of lake trout that spawned inside the refuge (Bronte et al. 1995).

I found that lake trout grew slower to a shorter asymptotic length inside the refuge than outside the refuge after 2000, in contrast to other studies that found larger individuals inside refuges (Halpern 2003; McClanahan et al. 2006; Lester and Halpern

2008). As survival increases inside and outside Gull Island refuge, growth decreases inside and outside. A refuge may favor increased species abundance, but an unexploited zone may reduce growth because a growing population within a refuge would increase pressure for limited resources and cannibalism within species (Halpern 2003), thereby reducing growth of individuals residing inside a refuge.

I found that lake trout matured at a similar length but at an older age inside the refuge than outside, and were similar in age at maturity to other lake trout populations prior to collapse, but older at maturity than other recovering lake trout populations in Lake Superior (Ferreri and Taylor 1996; Nieland et al. 2008). For example, a lake trout population recovering after high mortality reached 50% maturity at 6 years, based on a review of lake trout population dynamics during three periods: pre-lamprey introduction, lamprey invasion, and post-lamprey control (Ferreri and Taylor 1996). In contrast, 30% of lake trout captured in 1957, prior to sea lamprey control, exceeded age 9 at Gull Island Shoal (Swanson and Swedberg 1980). Lake trout were not older than age 9 in 1962, and did not exceed age 10 on the spawning reef until the early 1970s (Swanson and Swedberg 1980). The discrepancy between decades is likely caused by sea lamprey control that encouraged larger, older fish to reappear at GIS (Swanson and Swedberg 1980).

I found that mortality on lake trout was lower inside than outside the Gull Island refuge after 1992, likely because of years of freedom from exploitation, although mortality on lake trout inside and outside the refuge generally declined from 1981–1984 to 2001–2010. From 1963 to 1972, annual mortality on adult lake trout at Gull Island Shoal was 32.5% at age 8 and increased to 77.8% for fish age 10 and older (spawners longer than 29 inches; Swanson 1973). Similarly, annual mortality on native lake trout males on Gull Island Shoal during 1964−1976 ranged from 57% for fish age 8 and 9 to 73% for 10 and older spawners (Swanson and Swedberg 1980). Between 1981 and 1984, spring lake trout sampling was generally in offshore waters, in areas of low commercial and recreational fishing effort, but starting in 1985, sampling included inshore areas where commercial and recreational fishing was heavier. Therefore, annual mortality was higher inshore than offshore, where lake trout mortality was 40.2% and increased to 74.4% by 1986 (Schram 1986).

Compensatory density-dependent population regulation led to higher mortality, lower density, faster growth, earlier age to maturity, and longer asymptotic length of lake trout in areas not designated as a refuge from fishing (Ferreri and Taylor 1996; Rose et al. 2001). Similarly, in Michigan waters of Lake Superior, lake trout exposed to high mortality when sea lamprey dominated (1951−1961) were lower in abundance, grew faster, and were more fecund than when sea lamprey were controlled after 1962 (Ferreri and Taylor 1996). Although faster growth theoretically leads to younger age at maturity (Ferreri and Taylor 1996; Rose et al. 2001), lake trout residing in the Gull Island refuge grew slower to a shorter asymptotic length, but matured at an older age and similar length as lake trout residing outside the refuge. These outcomes don't necessarily point to an overcrowded population with stunted growth, but rather, a lake trout population still recovering in Wisconsin waters of Lake Superior, so the interaction between relative abundance, growth, maturity, and mortality have not yet reached equilibrium. Lake Superior historically sustained high lake trout abundance dominated by large-bodied, late-maturing individuals of several morphs, so the population could theoretically return to a similar status if protected from fishing mortality.

Reserving the integrity of Gull Island Shoal as a refuge has been imperative in maintaining lake trout abundance and stabilizing growth. Understanding source-sink theory and how it relates to aquatic ecosystems may be useful in comprehending lake trout population dynamics in Wisconsin waters of Lake Superior. A source population could persist without external larval supply, whereas a sink population would not persist (Bode et al. 2006). Previous research found that a source population does not change in population size, over several generations, but exports individuals. A sink is a net importer of individuals (Crowder 2000). Source-sink structure is often attributed to reef fish populations (Crowder 2000; Bode et al. 2006). Movement of reef-fish propagules is comparable to migrating adult fish moving from source to sink habitat. The source-sink theory in population dynamics came from the observation that not all habitat is of equal quality (Crowder 2000). Lake Superior has source-sink dynamic similar to other lakes. Lake trout move up to 42 km between spawning events across management units (Kapuscinski et al. 2005). Unprotected waters of Lake Superior are potential sinks and with little to no recruitment from protected areas, like Gull Island Shoal, so these populations would not be able to sustain commercial fishing yields. Recognizing where source and sink ecosystems are located is critical in identifying effective aquatic protective areas (Bode et al. 2006). No-take refuges placed in source habitat should act to strengthen the area as a demographic source, to redirect fishing to sink habitat that receive recruits from a source habitat. As long as sources are protected and fishing effort is reduced in areas with the greatest potential for exporting individuals, more fish and fishing opportunity is possible (Crowder 2000).

Management Implications

Our findings suggest that the lake trout population is dependent on the Gull Island refuge for protection of abundance, survival, and increasing age at maturity (9.9 years) to historical levels. Since the refuge was created, relative abundance of wild lake trout increased, survival increased, and annual growth decreased inside and outside the refuge during 1981−2010. I recommend that the refuge continue to be maintained to sustain benefits the refuge has provided since its establishment in 1976 and the likelihood of overexploitation of a source population of lake trout. Protection from overfishing is imperative for a species that has taken five decades to recuperate from near extirpation. The Gull Island refuge is a no-take haven for lake trout, but cisco and lake whitefish are exploited by commercial fisheries that also subject lake trout to unavoidable by-catch (WDNR 2011). Also, though growth slowed inside and outside the refuge, asymptotic length increased for lake trout outside the refuge, which is likely a positive effect of the refuge, but the only way to measure such benefits is to continue the refuge. Furthermore, this analysis excluded autumn data and does not include immigration of older, larger individuals during spawning. Previous research in Lake Michigan calculated dispersal radii for lake trout from spawning habitat and found emigration from the center of refuges to be at least 68 km (Schmalz et al. 2002). Lake Superior lake trout move at least 42 km between spawning events (Kapuscinski et al. 2005). Additionally, opening a refuge known as a source for fish and so close to a mainland would benefit those with fishing interests in Lake Superior, but opening a refuge that generates recruitment throughout western Lake Superior would disadvantage management and commercial fishing. Because commercial fishing is economically important and culturally established in Wisconsin waters, decisions regarding opening refuges to commercial use can be contrary to ecological health of an ecosystem. Immediate benefits anticipated by the public when opening a refuge to fishing often outweighs long-term benefits not fully conceptualized as valuable to all parties involved (Crowder 2000).

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TABLE 1.—Average asymptotic length (L_∞ = in), instantaneous rate at which length at age approaches L_∞ (K = 1/yr), theoretical age at length zero (t_0 = yr), and annual growth rate (ω = in/yr) of lake trout sampled inside and outside the Gull Island refuge in the Apostle Islands region of Lake Superior in four periods during 1981–2010. LL = lower 95% confidence limit and UL = upper 95% confidence limit of each parameter estimate.

		Inside			Outside		
Period	Parameter	Estimate	LL	UL	Estimate	LL	UL
1981–1984	L_∞	35.9	25.8	46.0	53,081.6	---	---
	K	0.203	0.027	0.378	0.000	---	---
	t_0	1.449	−0.134	3.031	−4.159	---	---
	ω	7.3	2.9	11.6	2.1	---	---
1985–1992	L_∞	33.3	28.9	37.7	33.2	32.0	34.3
	K	0.158	0.078	0.239	0.165	0.143	0.186
	t_0	−0.460	−2.032	1.113	0.211	−0.146	0.569
	ω	5.3	3.2	7.3	5.5	4.9	6.0
1993–2000	L_∞	29.4	27.7	31.2	33.1	30.8	35.5
	K	0.238	0.140	0.336	0.134	0.108	0.160
	t_0	2.064	0.702	3.426	0.112	−0.246	0.470
	ω	7.0	4.4	9.6	4.4	3.9	5.0
2001–2010	L_∞	31.5	30.1	32.8	34.1	32.0	36.2
	K	0.145	0.123	0.167	0.104	0.083	0.126
	t_0	0.539	0.139	0.939	−0.902	−1.566	−0.239
	ω	4.6	4.0	5.1	3.6	3.0	4.1

TABLE 2.—Maturity status of individual lake trout (1 = sexually mature; 2 = sexually immature) as a logistic function of length or age (b_0 = intercept; b_1 = slope) and length ($L_{0.5}$) and age ($A_{0.5}$) at 50% maturity inside (N = 197) and outside (N = 900) the Gull Island refuge in the Apostle Islands region of Lake Superior during 2001–2010. LL = lower 95% confidence limit and UL = upper 95% confidence limit of each parameter estimate.

		Inside			Outside		
Model	Parameter	Estimate	LL	UL	Estimate	LL	UL
Length	b_0	−12.374	−17.35	−9.246	−13.234	−15.09	−11.802
	b_1	0.556	0.412	0.784	0.604	0.537	0.691
	$L_{0.5}$	22.2	21.5	23.0	21.9	21.6	22.2
Age	b_0	-5.413	−7.394	−4.088	-5.488	−6.3	−4.84
	b_1	0.549	0.393	0.767	0.621	0.538	0.719
	$A_{0.5}$	9.9	9.2	10.8	8.8	8.5	9.2

TABLE 3.—Number of age-0 lake trout (N_0), instantaneous total mortality (Z), annual survival rate (S), and annual total mortality rate (A) of lake trout sampled inside and outside the Gull Island refuge in the Apostle Islands region of Lake Superior in four periods during 1981–2010. LL = lower 95% confidence limit and UL = upper 95% confidence limit of each parameter estimate.

		Inside			Outside		
Period	Parameter	Estimate	LL	UL	Estimate	LL	UL
1981–1984	$\text{Log}_e(N_0)$	9.632	6.861	12.404	9.816	8.266	11.366
	N_0	15,252	954	243,787	18,323	3,888	86,348
	Z	0.721	0.449	0.992	0.785	0.633	0.937
	A	51.4%	36.2%	62.9%	54.4%	46.9%	60.8%
	S	48.6%	37.1%	63.8%	45.6%	39.2%	53.1%
1985–1992	$\text{Log}_e(N_0)$	10.979	10.207	11.751	11.674	9.900	13.447
	N_0	58,630	27,098	126,855	117,420	19,927	691,885
	Z	0.591	0.532	0.651	0.635	0.498	0.771
	A	44.6%	41.2%	47.8%	47.0%	39.2%	53.8%
	S	55.4%	52.2%	58.8%	53.0%	46.2%	60.8%
1993–2000	$\text{Log}_e(N_0)$	7.388	6.641	8.135	9.266	8.357	10.176
	N_0	1,616	766	3,410	10,576	4,260	26,257
	Z	0.319	0.270	0.368	0.468	0.408	0.528
	A	27.3%	23.6%	30.8%	37.4%	33.5%	41.0%
	S	72.7%	69.2%	76.4%	62.6%	59.0%	66.5%
2001–2010	$\text{Log}_e(N_0)$	6.234	5.566	6.901	8.839	8.425	9.254
	N_0	510	261	993	6,901	4,559	10,446
	Z	0.244	0.198	0.289	0.391	0.363	0.419
	A	21.6%	18.0%	25.1%	32.3%	30.4%	34.2%
	S	78.4%	74.9%	82.0%	67.7%	65.8%	69.6%

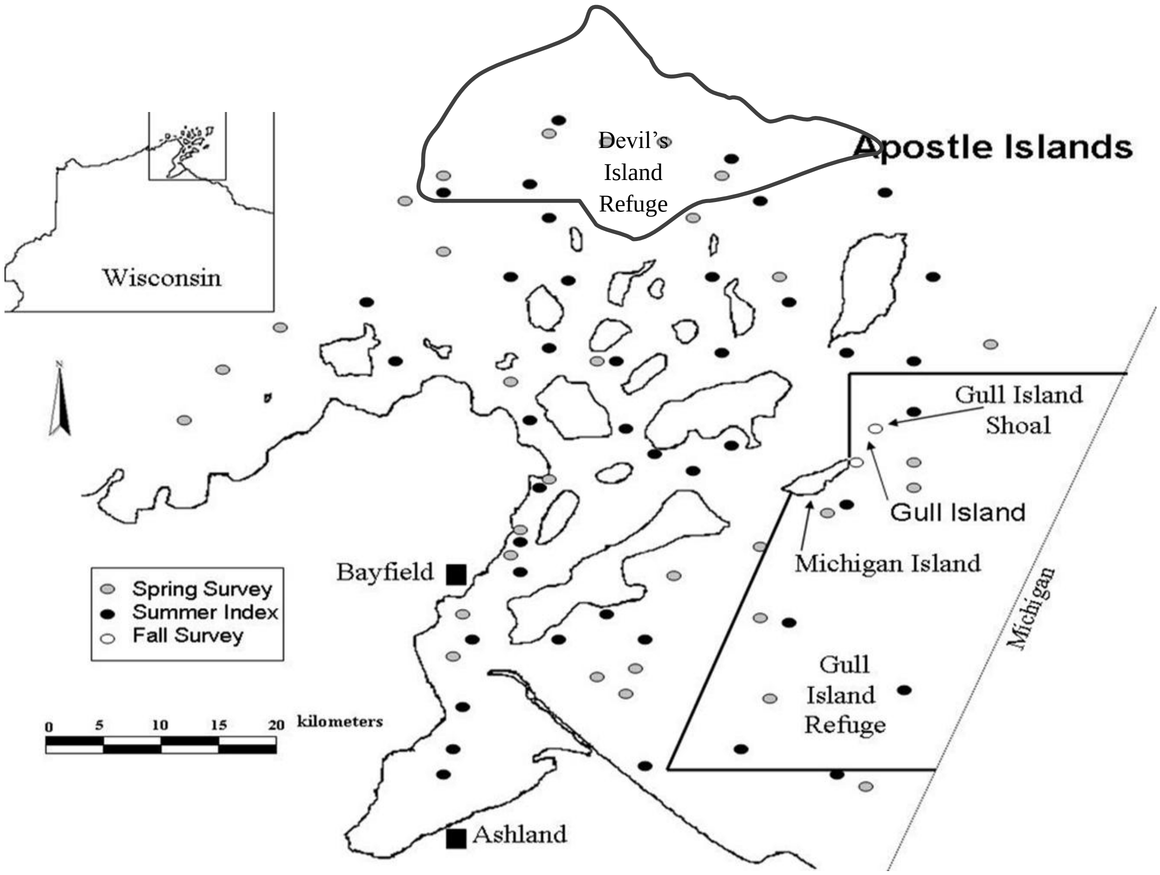

FIGURE 1.—Randomized stations for spring large-mesh, summer graded-mesh, and autumn large-mesh lake trout surveys in Gull Island (right) and Devil's Island (left) refuges in the Apostle Islands region of Wisconsin waters of Lake Superior.

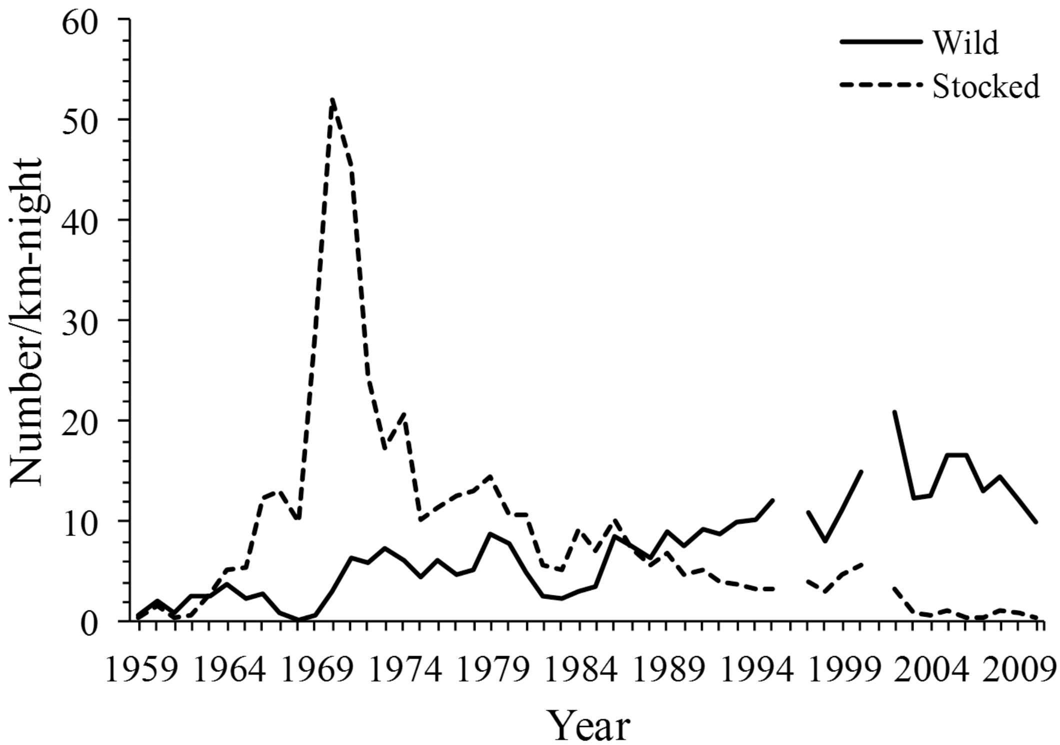

FIGURE 2.—Geometric-mean catch/km-night of wild and stocked lake trout during spring large-mesh gill-netting in the Apostle Islands region of Lake Superior during 1959–2010 (no sampling during gaps in years).

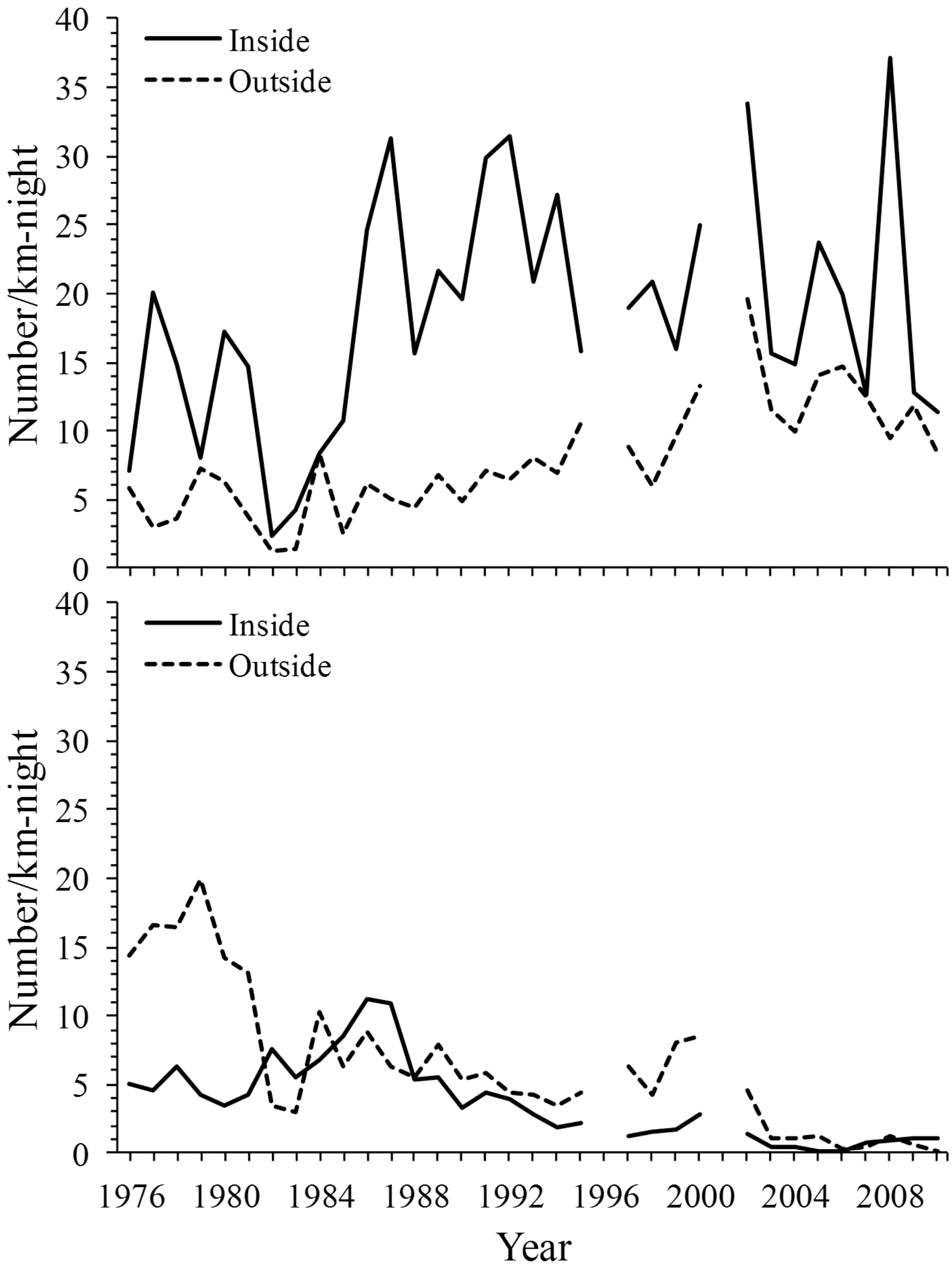

FIGURE 3.—Geometric-mean catch/km-night of wild (upper panel) and stocked (lower panel) lake trout during spring large-mesh gill-netting inside and outside the Gull Island refuge in the Apostle Islands region of Lake Superior during 1976–2010 (gaps = no sampling).

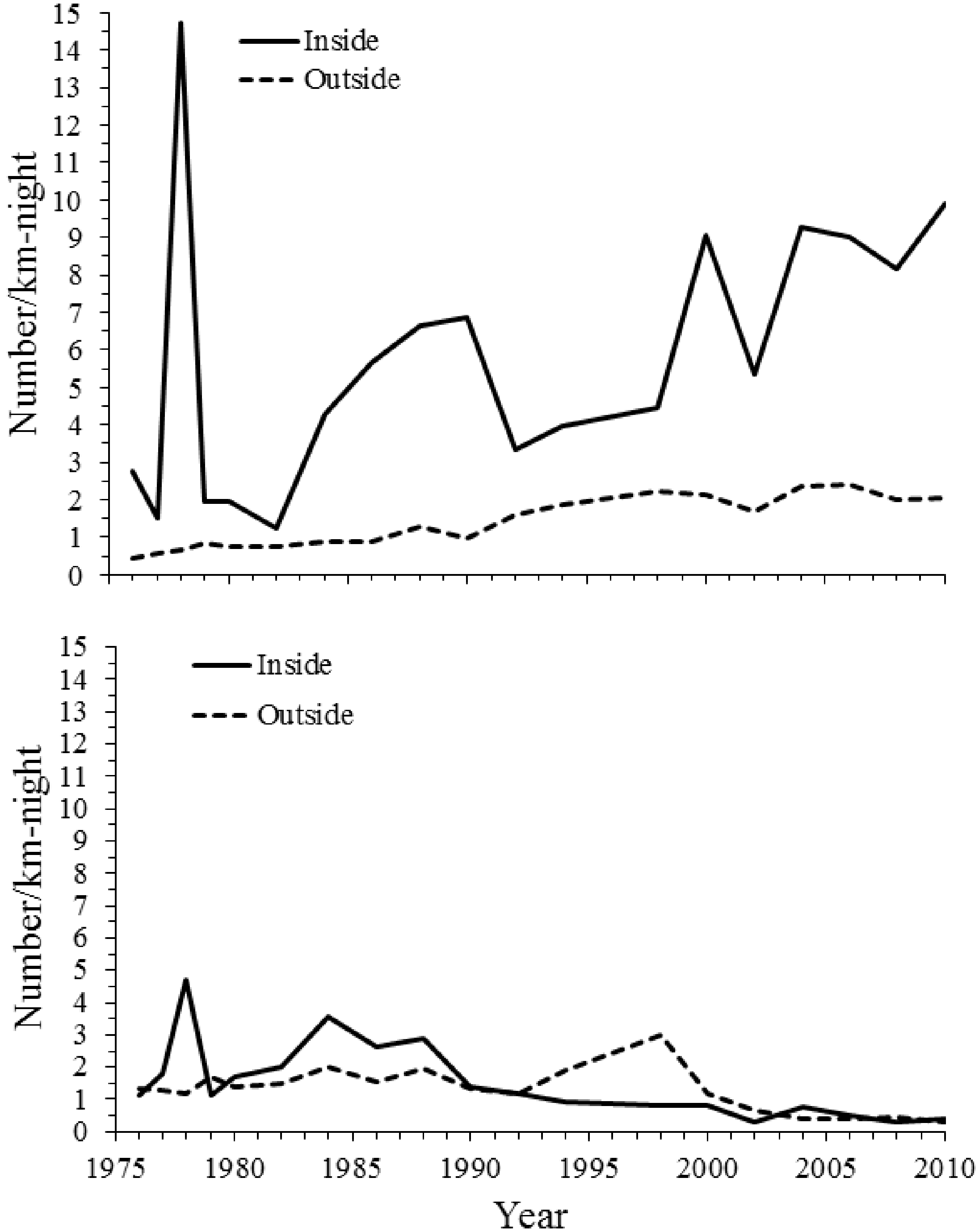

FIGURE 4.—Geometric-mean catch/km-night of wild (upper panel) and stocked (lower panel) lake trout during summer graded-mesh gill-netting inside and outside the Gull Island refuge in the Apostle Islands region of Lake Superior during 1976–2010.

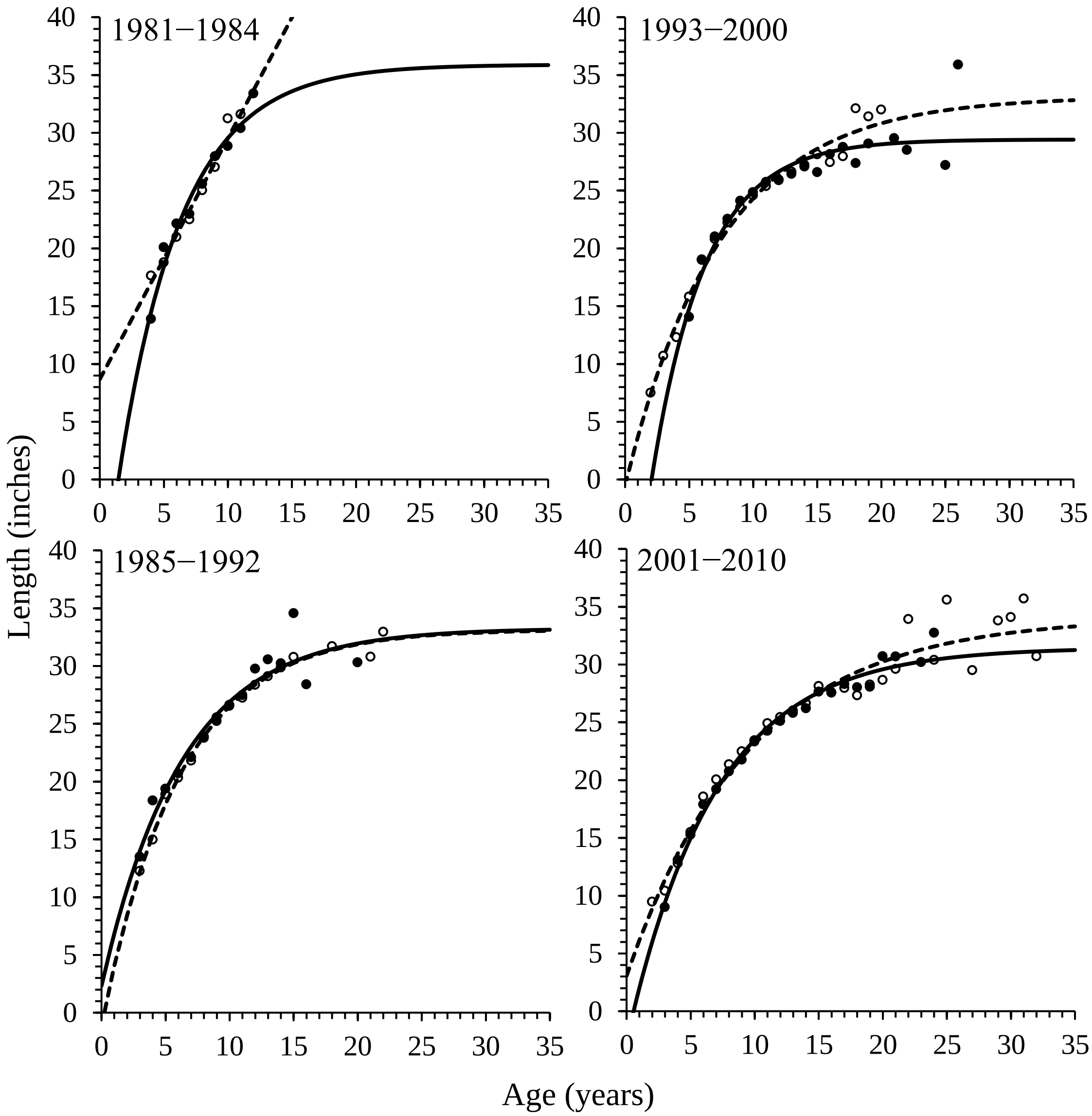

FIGURE 5.—Mean length at age of capture (symbols) and length-age curves (lines) for lake trout sampled inside (solid dots and lines) and outside (open dots and dashed lines) the Gull Island refuge in the Apostle Islands region of Lake Superior in four periods of 1981–2010.

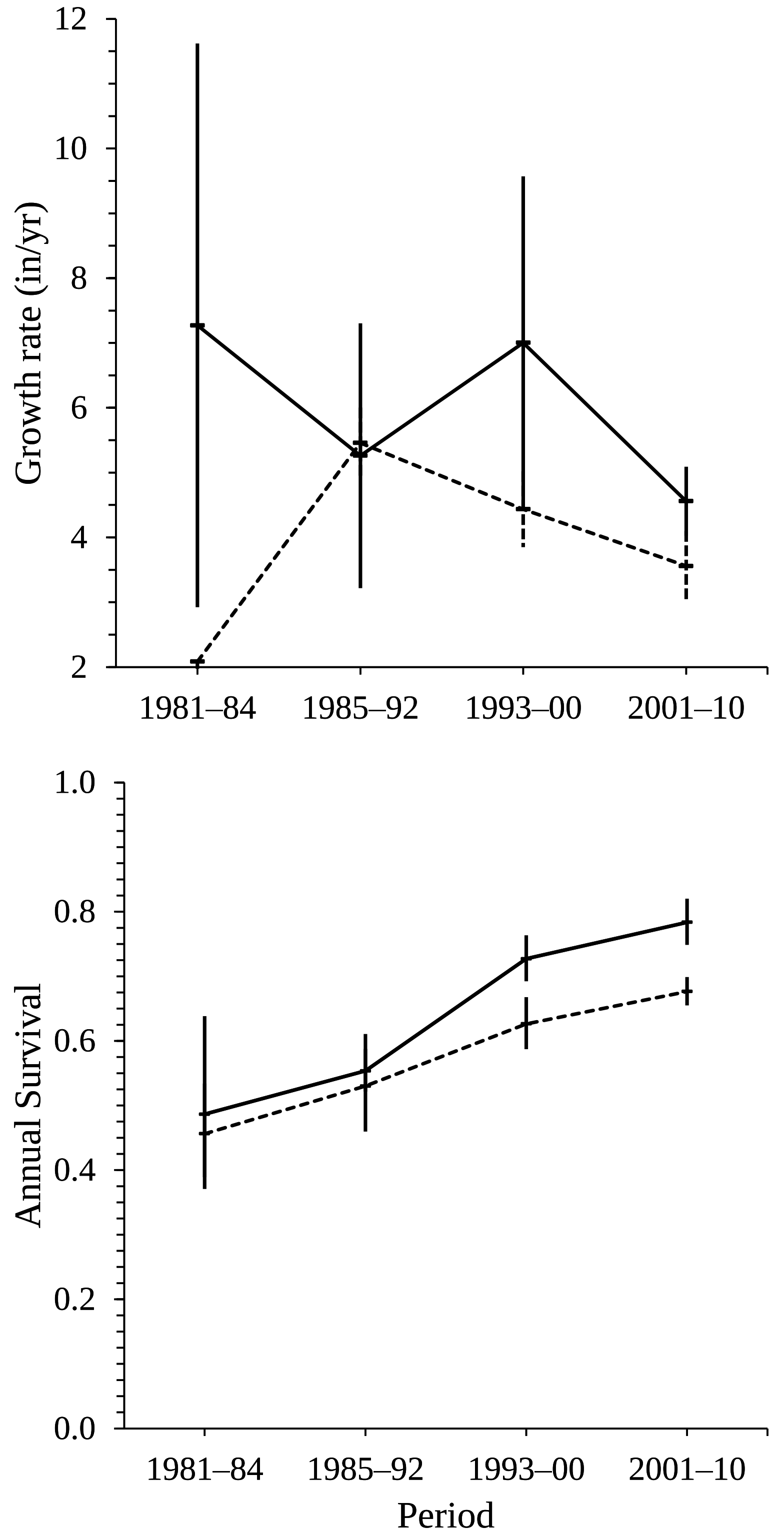

FIGURE 6.—Annual growth (upper panel) and survival (lower panel) of lake trout sampled inside (solid lines) and outside (dashed lines) the Gull Island refuge in the Apostle Islands region of Lake Superior during 1981–2010.

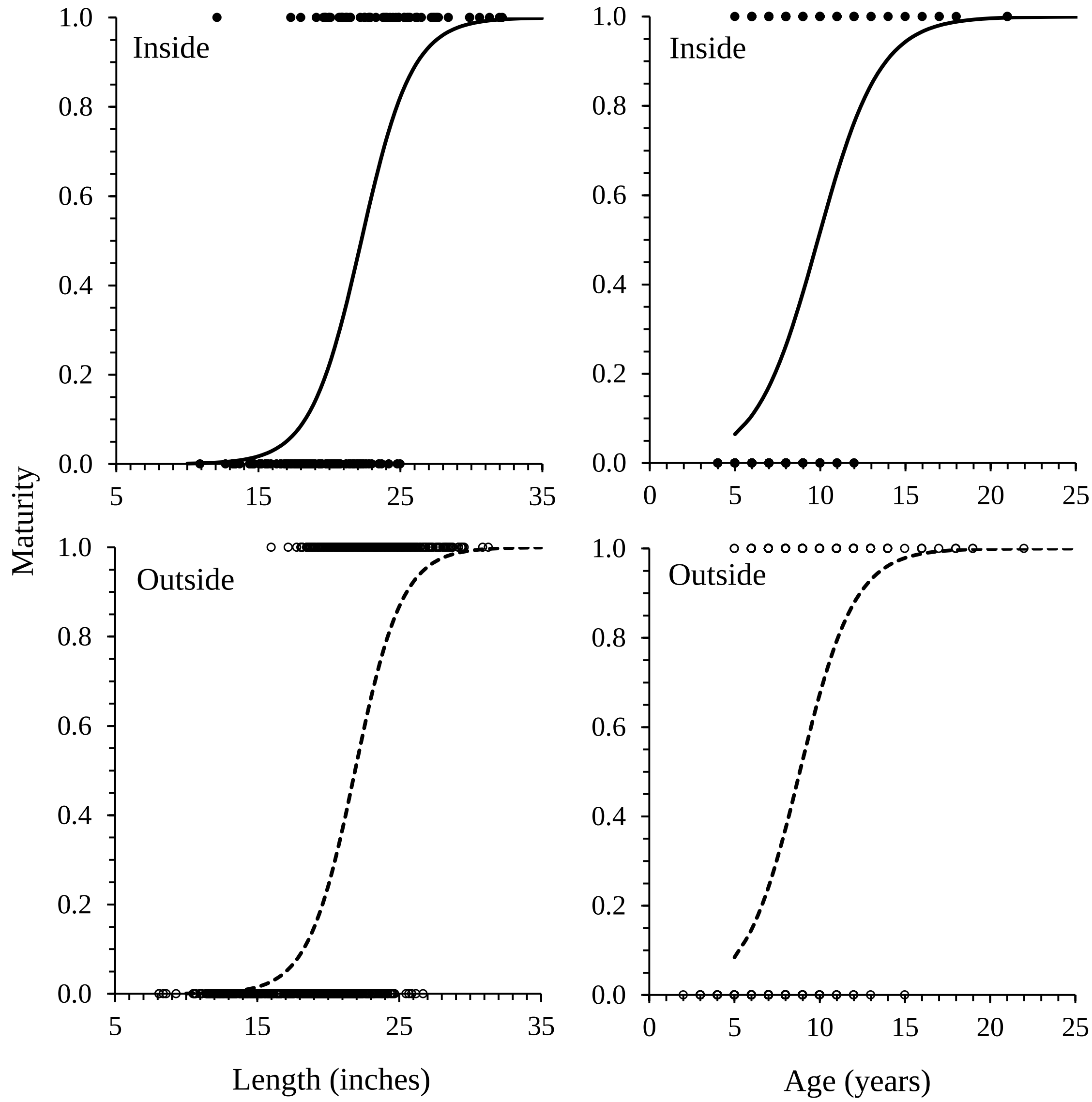

FIGURE 7.—Maturity at length and age and maturity curves for lake trout sampled inside (upper row = solid dots and lines) and outside (lower row = open dots and dashed lines) the Gull Island refuge in the Apostle Islands region of Lake Superior in 2001–2010.

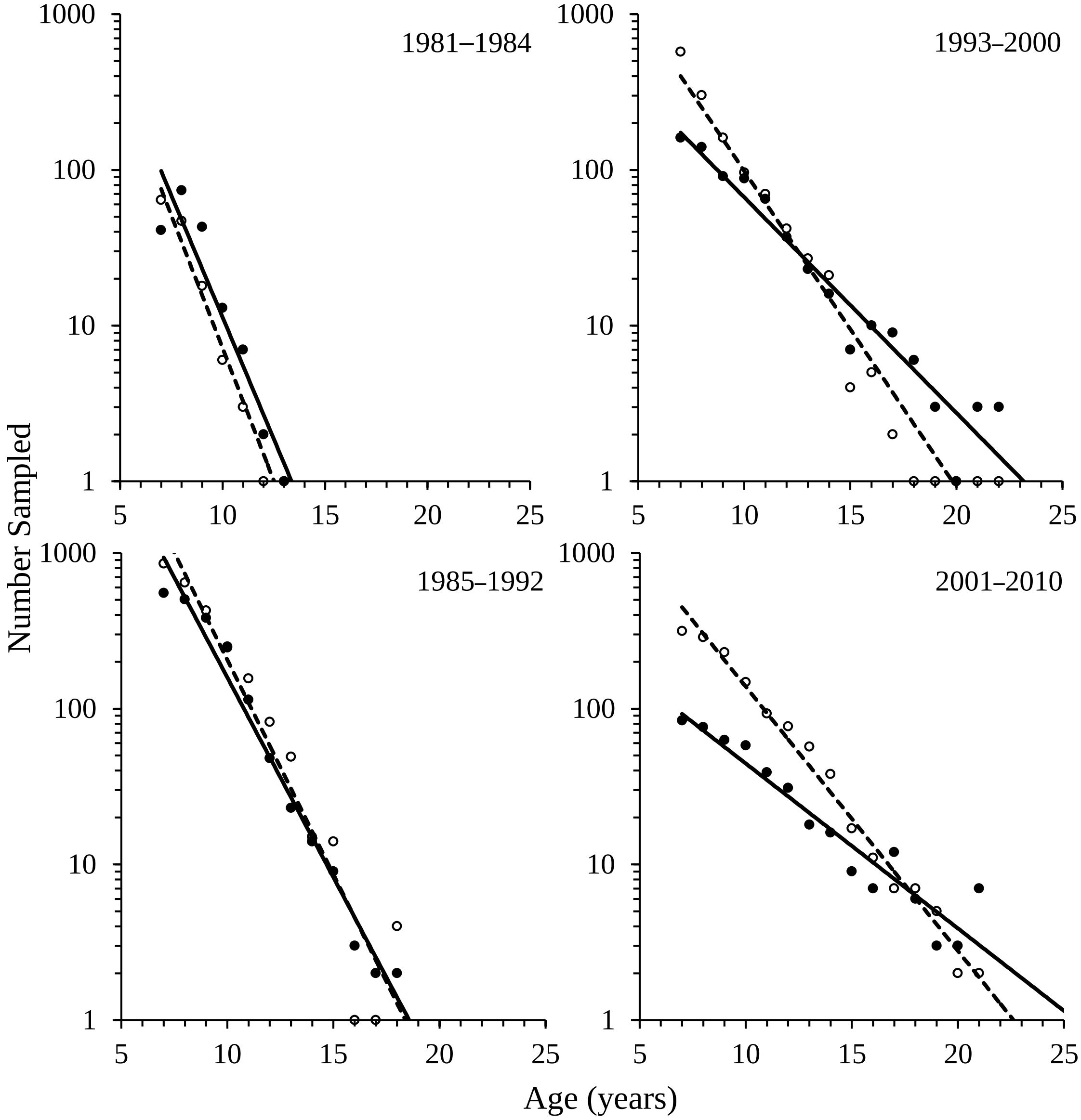

FIGURE 8.—Catch at age (symbols) and catch-curves (lines) for lake trout sampled inside (solid dots and lines) and outside (open dots and dashed lines) the Gull Island refuge in the Apostle Islands region of Lake Superior in four periods of 1981–2010.