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ARTICLE

Effectiveness of a Refuge for Lake Trout in Western Lake Superior II: Simulation of Future Performance

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Abstract
Historically, Lake Superior supported one of the largest and most diverse Lake Trout *Salvelinus namaycush* fisheries in the Laurentian Great Lakes, but Lake Trout stocks collapsed due to excessive fishery exploitation and predation by Sea Lampreys *Petromyzon marinus*. Lake Trout stocking, Sea Lamprey control, and fishery regulations, including a refuge encompassing Gull Island Shoal (Apostle Islands region), were used to enable recovery of Lake Trout stocks that used this historically important spawning shoal. Our objective was to determine whether future sustainability of Lake Trout stocks will depend on the presence of the Gull Island Shoal Refuge. We constructed a stochastic age-structured simulation model to assess the effect of maintaining the refuge as a harvest management tool versus removing the refuge. In general, median abundances of age-4, age-4 and older (age-4+), and age-8+ fish collapsed at lower instantaneous fishing mortality rates (*F*) when the refuge was removed than when the refuge was maintained. With the refuge in place, the *F* that resulted in collapse depended on the rate of movement into and out of the refuge. Too many fish stayed in the refuge when movement was low (0–2%), and too many fish became vulnerable to fishing when movement was high ($\geq$22%); thus, the refuge was more effective at intermediate rates of movement (10–11%). With the refuge in place, extinction did not occur at any simulated level of *F*, whereas refuge removal led to extinction at all combinations of commercial *F* and recreational *F*. Our results indicate that the Lake Trout population would be sustained by the refuge at all simulated *F*-values, whereas removal of the refuge would risk population collapse at much lower *F* (0.700–0.744). Therefore, the Gull Island Shoal Refuge is needed to sustain the Lake Trout population in eastern Wisconsin waters of Lake Superior.

Great Lakes populations of Lake Trout *Salvelinus namaycush* sustained fisheries until the early 1800s, when commercial and recreational fisheries depleted local stocks and expanded farther from shore into deeper waters to pursue new stocks—a process known as “fishing up” (Lawrie and Rahrer 1972; Goodier 1989). Fishing effort shifted from Lake Huron to Lake Michigan and finally to Lake Superior as Lake Trout stocks were depleted sequentially by the fisheries (Hansen 1999). In Lake Superior, the annual harvest averaging 2 million kg from 1879 to 1950 seemed sustainable, but advances in fishing technology caused Lake Trout yield to be sustained despite declining abundance (Hile et al. 1951; Pycha and King 1975). Because Lake Trout are long lived, slow growing, and late maturing, the level of exploitation exerted in the 1900s was not sustainable (Russ and Alcala 1996). Invasion by the Sea Lamprey *Petromyzon marinus* added pressure to already depleted Lake Trout populations, contributing to stock collapses in Lake Huron by 1947, in

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Lake Michigan by 1949, and in Lake Superior by 1960 (Hansen 1999).

To restore Lake Trout populations, stocking of hatchery-origin fish was used to bolster failing recruitment, while stringent harvest regulations and Sea Lamprey control were used to reduce mortality of adult fish (Lawrie and Rahrer 1973; Hansen et al. 1995; Linton et al. 2007). In the Apostle Islands region of Lake Superior, harvest-free zones (refuges) were established at Gull Island Shoal in 1976 and at Devils Island Shoal in 1981 (Swanson and Swedberg 1980; Schram et al. 1995; Nieland et al. 2008). Harvest-free zones are designed to facilitate the recovery of exploited stocks by protecting older, larger individuals (spawning biomass) while aiding the recruitment of younger, smaller individuals; these zones preserve or increase genetic diversity, age structure, and population size and provide recruitment to adjacent areas (Carr and Reed 1993; Man et al. 1995; Russ and Alcala 1996; Lauck et al. 1998; Agardy 2000; Halpern 2003). By 1996, Lake Trout stocks across much of Lake Superior, including the Apostle Islands region, had been rebuilt to the point where stocking became unnecessary (Schreiner and Schram 1997; Muir et al. 2012).

Our objective was to determine whether the future sustainability of Lake Trout in the Apostle Islands region of Lake Superior depends on the presence of the Gull Island Shoal Refuge. In western Lake Superior, Lake Trout stocks are building toward carrying capacity, so stocks that are protected by the refuge may be able to sustain fishery harvest (Corradin et al. 2008). Furthermore, a fishing agreement that regulates state and tribal fisheries in the Apostle Islands region expires in 2015, so discussion is expected on the efficacy and necessity of the Gull Island Shoal Refuge. Therefore, we constructed a stochastic age-structured simulation model to assess the effect of maintaining versus removing the refuge on Lake Trout stocks' sustainability in western Lake Superior. We evaluated the refuge's effects on the abundances of (1) age-4 fish as a measure of recruitment; (2) age-4 and older (age-4+) fish as a measure of the population vulnerable to fishing; and (3) age-8+ fish as a measure of the spawning population. This was accomplished by simulating the median Lake Trout abundance, the probability of stock collapse, and the time to extinction. We expected to find that the refuge is crucial for sustaining Lake Trout stocks in eastern Wisconsin waters of Lake Superior.

METHODS

Study area.—Lake Superior contains 10% of the world's surface freshwater, including more than half of the water in the Laurentian Great Lakes, and has the largest surface area of any freshwater lake in the world (82,414 km^2; Hansen et al. 1995). Lake Superior has a relatively low mean temperature ($\leq$6°C), deep water (maximum = 406 m; mean = 148 m), low dissolved solids (~60 mg/L), low average annual fish yield (0.8 kg/ha), and low primary productivity (1.6–5.6 mg C·m^{-3}·h^{-1}·month^{-1}), resulting in a highly oligotrophic state (Hansen et al. 1995). The lake supports 88 species of fish, 19 of which are nonnative (Habermann et al. 2012). The Lake Trout is the apex predator (Hansen et al. 2005).

Lake Superior is partitioned into management zones for regulating Lake Trout fisheries (Figure 1). Wisconsin waters are divided into two Lake Trout management zones: the

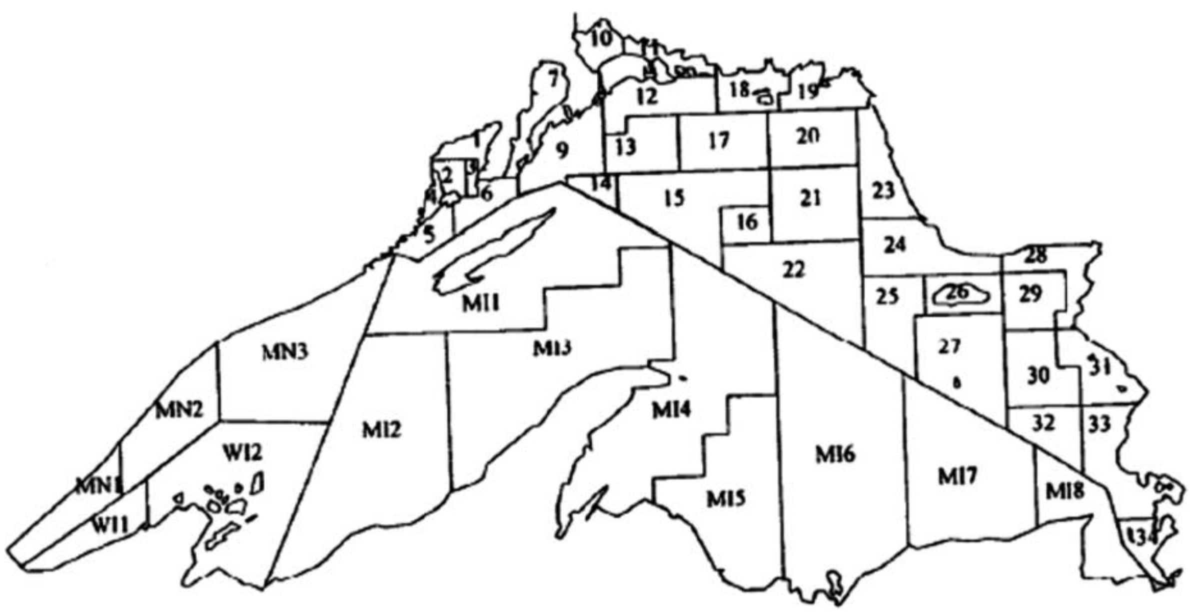

FIGURE 1. Lake Trout management areas in Lake Superior. United States management areas are denoted with the abbreviation for each state (MI = Michigan; MN = Minnesota; WI = Wisconsin). Canadian management areas are designated only with numbers.

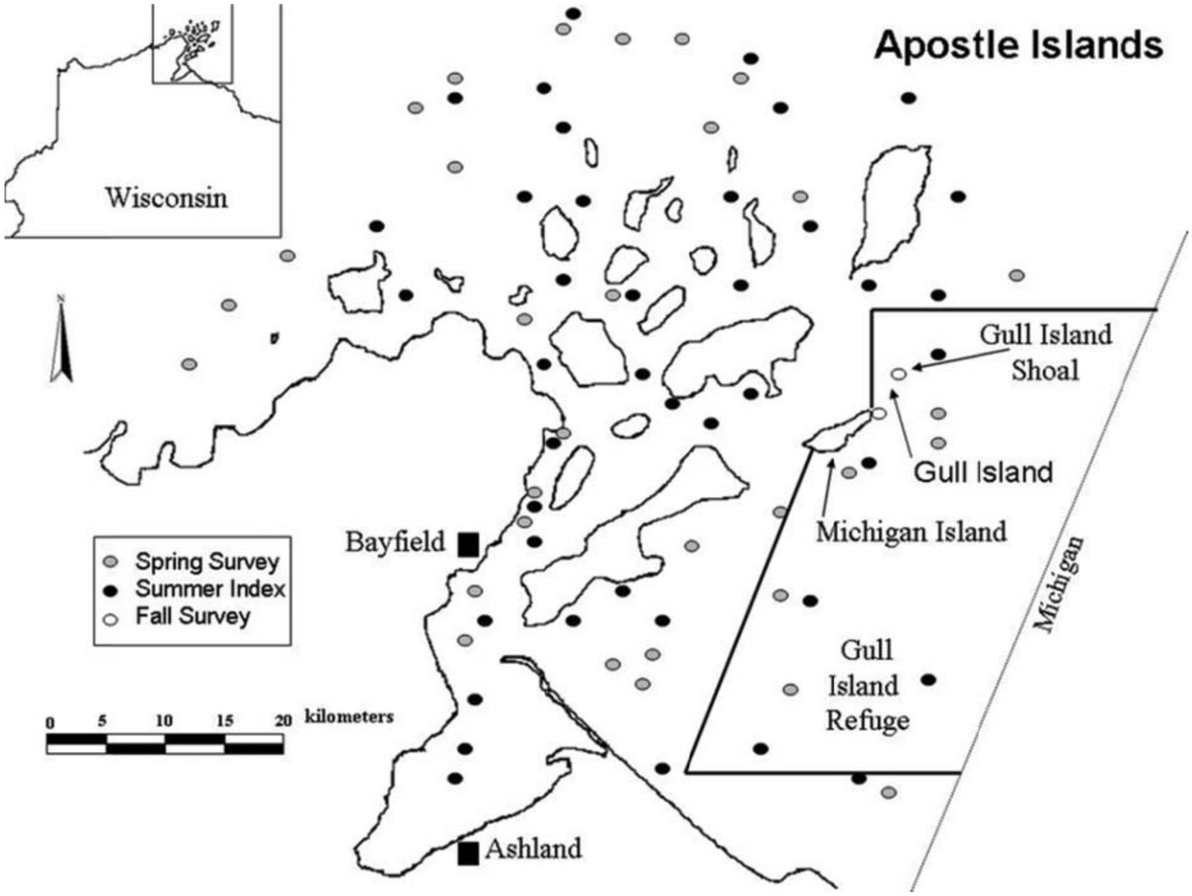

FIGURE 2. Location of the Gull Island Shoal Refuge (and survey stations) in the Apostle Islands region within Wisconsin waters of Lake Superior.

western portion (WI-1) and the Apostle Islands region (WI-2). Zone WI-2 contains the Gull Island Shoal Refuge; more sport fishing, commercial fishing, and surveying effort than WI-1; and the 22 Apostle Islands, which encompass 4,473 km^2 (2,612 km^2 with suitable depths [$\leq$73 m] for Lake Trout; Hansen et al. 1996). Water depth is shallow (generally $<$ 65 m), except for a 140-m trench along the eastern boundary of the islands. The Apostle Islands region has two refuges where commercial and recreational fishing are prohibited: the Gull Island Shoal Refuge (336 km^2) and the Devil's Island Shoal Refuge (283 km^2; Figure 2; Hansen et al. 1995; Linton et al. 2007).

The Gull Island Shoal Refuge contains the shoal, Gull and Michigan islands, and a nursery area near the eastern edge of the Apostle Islands region (Figure 2). Spawning habitat ranges in depth from 1 to 20 m, is surrounded by water deeper than 70 m, and covers an area nearly 3,100 ha. Nursery habitat ranges in depth from 10 to 40 m and is surrounded by water deeper than 70 m. The nursery habitat consists mainly of sand substrate, with some isolated rock ridges (Bronte et al. 1995; Schram et al. 1995). Age-0 Lake Trout move to the Michigan Island nursery area from the spawning habitat at Gull Island Shoal (Bronte et al. 1995).

Model structure.—We devised an age-structured population model for the wild Lake Trout population in Wisconsin waters of Lake Superior to simulate future population status under scenarios of refuge presence (i.e., the Gull Island Shoal Refuge is maintained in the future) and refuge absence (i.e., the refuge is removed/abandoned in the future; Figure 3; Nieland 2006). The simulation model was parameterized using statistical catch-at-age (SCAA) model estimates for recreational and commercial fishery harvest, abundance at age, age-specific mortality, year-specific mortality, gear selectivity, catchability, and assessment catch per effort (CPE) for age-4+ wild Lake Trout populations in non-refuge waters of Lake Superior zone WI-2 during 1980–2001 (Tables 1, 2; Linton et al. 2007). The Wisconsin Department of Natural Resources (WDNR) subsequently updated the SCAA model through 2012 (M. J. Seider, WDNR, unpublished data). Median abundance, probability of collapse, and time to extinction were used to evaluate sustainability of the Lake Trout population when subjected to a range of fishing mortality rates (F). The model was used to simulate the probability distributions of population metrics over a range of size-selective total annual mortality rates that mimicked the presence or absence of the refuge as a control on Lake Trout fishing mortality. The model

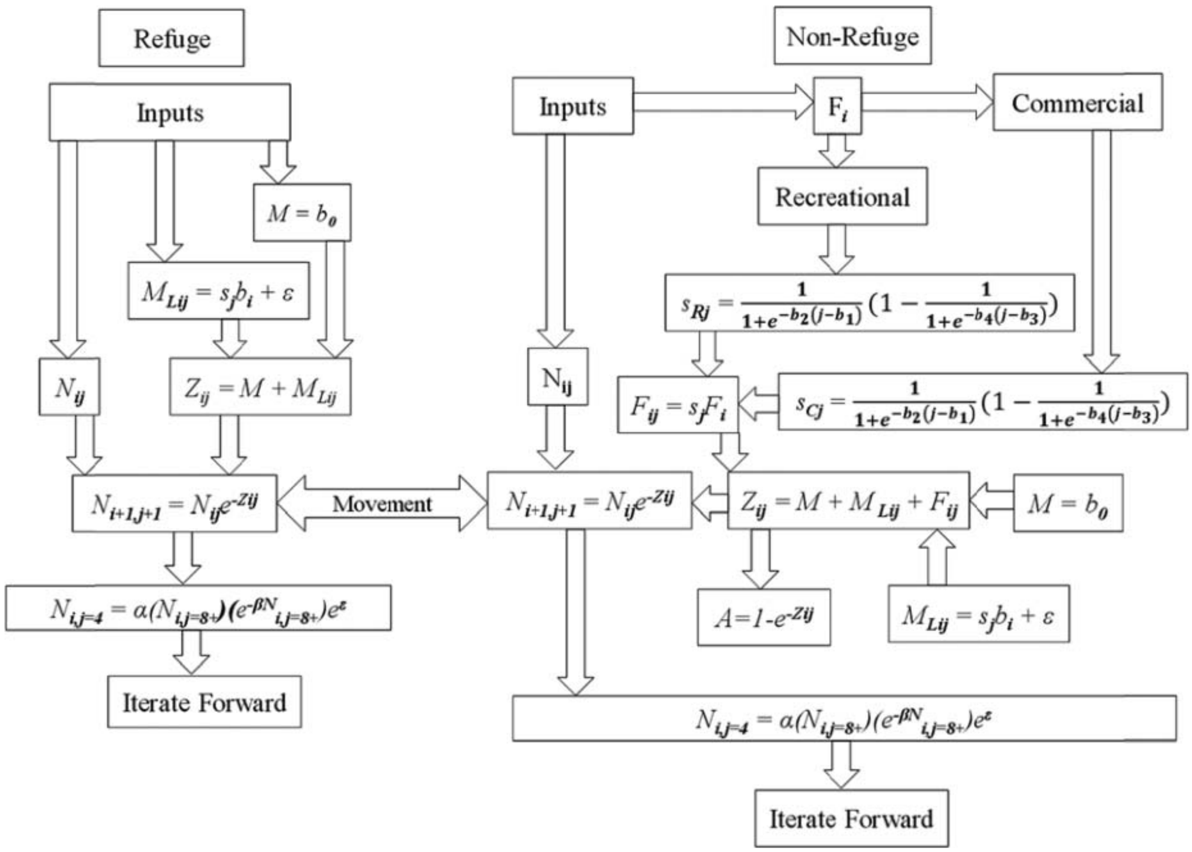

FIGURE 3. Schematic diagram of a model used for simulating future Lake Trout abundance in eastern Wisconsin waters of Lake Superior (i = year; j = age; F_i = total instantaneous fishing mortality rate in year i; N_{ij} = initial abundance of age j in year i; A = total annual mortality; see Methods text for definitions of other symbols).

included two stocks: one that was subjected to fishing and one that was protected from fishing.

Initial abundance (N_{ij}) at age j for year $i = 0$ in the simulation model was derived from age-specific estimates of wild Lake Trout abundance from the SCAA model for 2012. The SCAA model estimates abundance for non-refuge waters only, so a refuge submodel was created by using area-weighted spring gill-net CPE data. First, we determined the non-refuge surface area of WI-2 and the surface area of the Gull Island Shoal Refuge. We then multiplied CPE estimates from refuge and non-refuge waters by the corresponding surface areas to produce area-weighted CPEs. Next, we divided the area-weighted CPEs for the refuge by the area-weighted CPEs for non-refuge waters and multiplied the resulting ratio by the SCAA model estimate of non-refuge abundance for fully vulnerable (age-7+) Lake Trout in each year; this provided an estimate for the refuge abundance of age-7+ Lake Trout. Lastly, we apportioned the estimated refuge abundance into age-classes by using age frequency data from large-mesh gill-net surveys. Age-specific abundance estimates for 2012 were used to predict abundance at age in the next year,

$$N_{i+1,j+1} = N_{ij}e^{-Z_{ij}},$$

where $N_{i+1,j+1}$ is the number of Lake Trout surviving in each age-class j and year i to the next age-class ($j + 1$) and year ($i + 1$); N_{ij} is the number of Lake Trout in age-class j in year i; and Z_{ij} is the total instantaneous mortality rate for each age-class j in year i (Figure 3; Quinn and Deriso 1999; Haddon 2001). The Z_{ij} was the sum of (1) the total instantaneous natural mortality rate (M) previously estimated as a constant over all ages and years in the SCAA model (M = 0.11474); (2) the instantaneous mortality rate due to Sea Lamprey predation (M_{Lij}) for Lake Trout age-class j in year i; and (3) the total instantaneous fishing mortality rate (F_{ij}) for age-class j in year i,

$$Z_{ij} = M + M_{Lij} + F_{ij}.$$

We modeled M_{Lij} as a simple random variable based on the mean (b_0) and SD (ε) of fully selected Sea Lamprey-based mortality estimated from the SCAA model during 1980–2012 and wounding rates,

$$M_{Lij} = s_j b_0 + \varepsilon,$$

where s_j is the relative selectivity of Sea Lamprey mortality for each age-class j, which was derived from the average of the ratios

TABLE 1. Age-specific parameter values for a stochastic age-structured simulation model of Lake Trout in eastern Wisconsin waters (management zone WI-2) of Lake Superior (M_L = Sea Lamprey predation mortality).

Parameter	Abundance in non-refuge waters	Abundance in refuge waters	M_L selectivity
N_0	829,922	13,583	0.000
N_1	696,049	11,392	0.000
N_2	583,771	9,555	0.000
N_3	489,604	8,014	0.000
N_4	32,218	6,722	0.051
N_5	364,936	5,941	0.116
N_6	89,395	5,086	0.191
N_7	397	3,948	0.305
N_8	49,435	17,066	0.401
N_9	16,713	20,381	0.510
N_{10}	440	2,074	0.634
N_{11}	2,555	6,226	0.719
N_{12}	420	1,825	0.745
N_{13}	1,242	1,755	0.839
N_{14}	1,049	1,395	0.924
N_{15}	429	3,263	1.000
N_{16}	1,856	769	1.000
N_{17}	2,484	1,685	1.000
N_{18}	4,450	1,286	1.000
N_{19}	2,160	2,629	1.000
N_{20}	3,536	1,531	1.000
N_{21}	2,703	2,470	1.000
N_{22}	818	2,218	1.000
N_{23}	365	650	1.000
N_{24}	1,482	659	1.000
N_{25}	333	980	1.000
N_{26}	232	307	1.000
N_{27}	105	83	1.000
N_{28}	74	154	1.000
N_{29}	87	129	1.000
N_{30}	18	28	1.000

of M_L for each age-class to b_0 the fully selected M_L for age-15+ Lake Trout from the SCAA model during 1980–2012. Instantaneous Sea Lamprey mortality for age-15+ Lake Trout was used as the fully selected M_L because SCAA estimates of Sea Lamprey selectivity increased with Lake Trout size to a maximum at age 15+ (Swink 1991, 2003).

The F of age-j Lake Trout in year i was separated into components for the commercial fishery (F_{Cij}) and the recreational fishery (F_{Rij}):

$$F_{ij} = F_{Cij} + F_{Rij}.$$

For the commercial gill-net fishery, F_{Cij} was the product of the fully selected instantaneous fishing mortality rate (F_{Ci}) in year i and the relative selectivity (s_{Cj}) of large-mesh gill nets

TABLE 2. Parameter values for a stochastic age-structured simulation model of Lake Trout in eastern Wisconsin waters (management zone WI-2) of Lake Superior (M = instantaneous natural mortality rate; M_L = Sea Lamprey predation mortality; F_C = commercial fishing mortality rate; F_R = recreational fishing mortality rate).

Parameter	Non-refuge waters	Refuge waters
M	0.11	0.11
M_L mean	0.11	0.11
M_L error	0.068	0.068
Starting F_C	0.41	0.41
Starting F_R	0.08	0.08
Recruitment scalar	0.20	0.15

for age-class j,

$$F_{Cij} = s_{Cj} F_{Ci},$$

where s_{Cj} is described as a gamma function. For the recreational fishery, F_{Rij} was likewise the product of fully selected instantaneous fishing mortality (F_{Ri}) and age-specific angling selectivity (s_{Rj}). Age-specific commercial and recreational selectivity values were estimated within the SCAA model (Figure 4).

Using a Ricker stock–recruitment model (Ricker 1975), the number of age-0 Lake Trout ($N_{i+1,j=0}$) that recruited to the population in each year i + 1 was predicted from the number of adults ($N_{i,j=8+}$) that spawned in the previous year i,

$$N_{i+1,j=0} = \alpha\left(N_{i,j=8+}\right)\left(e^{-\beta N_{i,j=8+}}\right)e^{\varepsilon},$$

where α is the recruits per adult at low adult density; $N_{i,j=8+}$ is the abundance of age-8+ Lake Trout in year i; β is the instantaneous decline in the recruitment rate as parental abundance

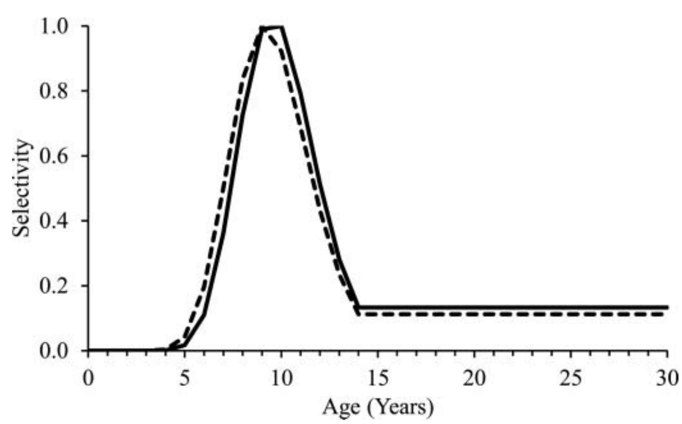

FIGURE 4. Age-specific selectivity of commercial gill-net fisheries (solid line) and recreational angling fisheries (dashed line) for Lake Trout in eastern Wisconsin waters of Lake Superior, 1980–2012 (J. Myers, Wisconsin Department of Natural Resources, unpublished data).

increases; and ε is process error. To account for parameter uncertainty, a different set of model parameters (α, β, and ε) was selected for each year and simulation from a Markov-chain Monte Carlo sample of the joint posterior probability distribution of parameter estimates (Nieland et al. 2008). To simplify model structure, we did not include process error autocorrelation, which was shown by Connors et al. (2014) to have a negligible effect on the misclassification of abundance declines in density-dependent models with process error and process error autocorrelation levels similar to those estimated for Lake Trout in WI-2 by Nieland et al. (2008)—especially at the high classification thresholds (>80% decline in abundance) and long observation windows (>60 years) we used to measure Lake Trout population sustainability (see simulation metrics below). Age-8+ Lake Trout were used to index spawning stock density because 50% of females reach sexual maturity at age 8 (Peck and Sitar 2000). A recruitment scalar was used for the refuge and non-refuge submodels to mimic abundances during 1980–2012. The refuge scalar was set as the ratio of WI-2 refuge area (336 km^2) to non-refuge area (2,276 km^2) with depths less than 73 m. The non-refuge scalar was set by trial and error to a constant that matched (1) the mean and SD of simulated abundances in simulation years 51–200 to (2) the mean and SD of SCAA-estimated abundances for 1980–2012.

Fish can move between refuge and non-refuge waters, so we estimated the movement rate as the percentage of fish that were marked during fall spawning surveys on Gull Island Shoal in a given year and that were later recaptured during surveys in non-refuge waters in the next year (Schram et al. 1995). First, the number of recaptured tags was expanded to the total number of tags present in non-refuge waters that originated from the previous autumn's tagging efforts within the refuge: the number of recovered tags was divided by the total catch, and the resulting value was multiplied by the non-refuge abundance estimate for each year. Next, to estimate the movement rate across refuge boundaries, the estimated number of refuge-origin tags in non-refuge waters was divided by refuge abundance to obtain the percentage of fish that originated from the refuge but that were captured outside the refuge. We repeated this for each year of the SCAA model (Figure 5). To account for uncertainty in the estimated movement rate, we simulated the population with zero movement, median movement, upper 97.5th-percentile movement, maximum movement, and two times the maximum movement (Table 3). To account for fish movement from non-refuge waters to refuge waters, we assumed that fish moved into the refuge from non-refuge waters at the same rate for all age-classes.

Simulations.—Ranges of Lake Trout movement rates and F-values were simulated to evaluate the effects of fish movement and fishing mortality allocations between recreational and commercial fishing on population sustainability. First, a constant value for fully selected F_C (0.4; the average annual SCAA estimate for 1980–2012) was tested over a range of fully selected F (0.0–1.8) by varying the fully selected F_R. Next, a constant value of fully selected F_R (0.1; again, the average annual SCAA estimate for 1980–2012) was tested over a range of fully selected F (0.0–1.8) by varying the fully selected F_C. Lastly, equal levels of fully selected F_C and F_R were tested over a range of fully selected F (0.0–1.8). The fishery was simulated 1,000 times for 200 years under each combination of F and movement rate (Nieland et al. 2008). Simulations recorded the fishable population of Lake Trout; therefore, fish in the refuge that moved into non-refuge waters, where they became susceptible to fishing mortality, were recorded as part of the non-refuge population. For simulations of refuge removal, fish in the refuge population were subjected to fishing and thus were added to the non-refuge population.

Median abundance, probability of collapse, and time to extinction were used to evaluate the sustainability of F. Median abundance was calculated as the median number of age-4

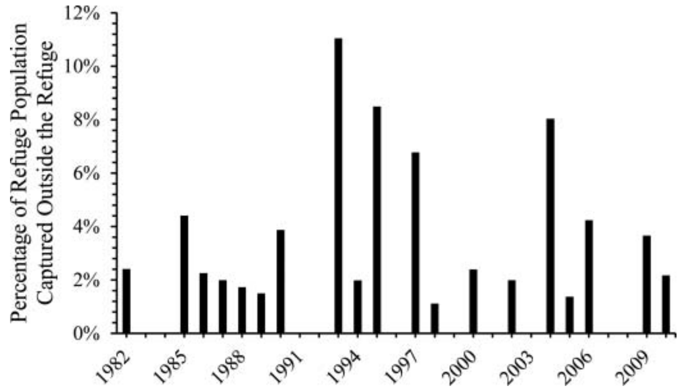

FIGURE 5. Movement rate (%) of Lake Trout from the Gull Island Shoal Refuge to non-refuge areas within eastern Wisconsin waters of Lake Superior, 1982–2010.

TABLE 3. Movement scenarios and fishing mortality combinations (F_C = commercial fishing mortality rate; F_R = recreational fishing mortality rate) simulated for the Lake Trout population in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration). The movement rate is the proportion of fish that moved from refuge waters to non-refuge waters (and vice versa). Each movement scenario was simulated for each combination of fishing mortality rates.

Movement		Fishing mortality		
Scenario	Rate	Combination	F_C	F_R
No movement	0.000	Constant F_C	0.4	0.05–1.4
Median	0.021	Constant F_R	0.2–1.7	0.1
Upper confidence limit	0.096	Equal F_C and F_R	0.1–0.9	0.1–0.9
Maximum	0.110			
2× maximum	0.220			
No refuge	0.000			

(recruits), age-4+ (fishable stock), and age-8+ (adults) Lake Trout in non-refuge waters from year 51 to year 200 for each simulation. The year of extinction for the Lake Trout population was defined as the first year in which age-4+ abundance was equal to zero. The probability of collapse was computed as the proportion of 1,000 simulations in which mean annual age-4+ and age-8+ abundances fell below 10% of the mean annual age-4+ and age-8+ SCAA-estimated abundances for 1980–2012 (i.e., >90% decline; Hansen et al. 2010). The F that resulted in stock collapse was used to assess the sustainability of the population for each scenario. The probability of collapse was computed using exact upper and lower 95% confidence limits for a binomial proportion (Zar 1999). The time to extinction was calculated as the median number of years until age-4+ abundance declined to zero. Simulations that did not result in extinction were assigned an extinction time of "$>$200 years." Confidence intervals were computed as the 2.5th and 97.5th percentiles of time to extinction for 1,000 simulations.

RESULTS

Lake Trout recruits (age 4) were better protected against stock collapse when the Gull Island Shoal Refuge was maintained than when it was removed. With the refuge present, the average number of recruits collapsed (depending on the movement rate) at an F of 0.619–1.725 when F_C and F_R were equal; at an F of 0.647–1.734 when F_C was constant; and at an F of 0.662–1.987 when F_R was constant (Figure 6; Table 4). In the absence of the refuge, recruit abundance reached collapse at an F of 0.71 under a scenario of equal F_C and F_R; at an F of 0.725 under a constant F_C; and at an F of 0.739 under a constant F_R (Figure 6; Table 4). When the refuge was maintained, a fixed F_R required a higher F to induce collapse than other combinations of fishing mortality (Table 4). With continued use of the refuge, age-4 abundance at an F of 0 declined as the movement rate increased from 0% to 22%, and the F that induced collapse peaked at movement rates between 10% and 15% (Figures 7, 8).

The fishable stock (age-4+) of Lake Trout was better protected against stock collapse when the refuge was present than when the refuge was removed. When the refuge was maintained, average numbers of age-4+ Lake Trout collapsed (depending on the movement rate) at an F of 0.624–1.630 under a scenario of equal F_C and F_R; at an F of 0.648–1.549 under a constant F_C; and at an F of 0.663–1.912 under a constant F_R (Figure 9; Table 4). With the refuge removed, fishable stock abundance declined to collapse at an F of 0.716 when F_C and F_R were equal; at an F of 0.729 when F_C was constant; and at an F of 0.744 when F_R was constant (Figure 9; Table 4). With the refuge present, age-4+ abundance at an F of 0 declined as the movement rate increased from 0% to 22%, and the F that induced collapse peaked at movement rates between 10% and 15% (Figures 7, 8).

Adult (age-8+) Lake Trout were more resilient against stock collapse when the refuge was maintained than when it was removed. With continued use of the refuge, the average number of adults collapsed (depending on the movement rate) at an F of 0.597–1.221 under a scenario of equal F_C and F_R; at an F of 0.623–1.200 under a constant F_C; and at an F of 0.643–1.365 under a constant F_R (Figure 10; Table 4). With removal of the refuge, adult abundance collapsed at an F of 0.7 when F_C and F_R were equal; at an F of 0.718 when F_C was constant; and at an F of 0.715 when F_R was constant (Figure 10; Table 4). When the refuge was present, age-8+ abundance at an F of 0 declined as the movement rate increased, and the F that induced collapse peaked at movement rates between 12% and 17% (Figures 7, 8). Abundance of age-8+ Lake Trout collapsed at a lower F than the abundance of either age-4 fish or age-4+ fish (Figure 7; Table 4).

Collapse of fishable (age-4+) and adult (age-8+) Lake Trout was induced by a higher F when the refuge was present than when the refuge was removed (except at a movement rate of zero), regardless of the movement rate or F (Figure 11). With the refuge present, collapse was induced at a lower F for adults than for fishable Lake Trout (except when the movement rate was zero); however, when the refuge was removed, age-4+ and age-8+ Lake Trout collapsed at similar levels of F (Figure 11). With continued use of the refuge, the F that induced

TABLE 4. Instantaneous fishing mortality rates (F) that induced collapse of age-4, age-4 and older (age-4+), and age-8+ Lake Trout at varying movement rates and fishing mortality combinations (F_C = commercial fishing mortality rate; F_R = recreational fishing mortality rate) in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration). The movement rate is the proportion of fish that moved from refuge waters to non-refuge waters (and vice versa).

		F		
Movement rate	Combination	Age 4	Age 4+	Age 8+
0.000	Constant F_C	0.647	0.648	0.623
	Constant F_R	0.662	0.663	0.643
	Equal F_C and F_R	0.619	0.624	0.597
0.021	Constant F_C	1.261	1.261	0.946
	Constant F_R	1.448	1.453	1.073
	Equal F_C and F_R	1.286	1.291	0.957
0.096	Constant F_C	1.734	1.642	1.200
	Constant F_R	1.987	1.912	1.365
	Equal F_C and F_R	1.725	1.630	1.221
0.110	Constant F_C	1.634	1.549	1.181
	Constant F_R	1.892	1.816	1.342
	Equal F_C and F_R	1.592	1.511	1.195
0.220	Constant F_C	1.280	1.248	1.077
	Constant F_R	1.435	1.400	1.185
	Equal F_C and F_R	1.303	1.273	1.108
No refuge	Constant F_C	0.725	0.729	0.718
	Constant F_R	0.739	0.744	0.715
	Equal F_C and F_R	0.710	0.716	0.700

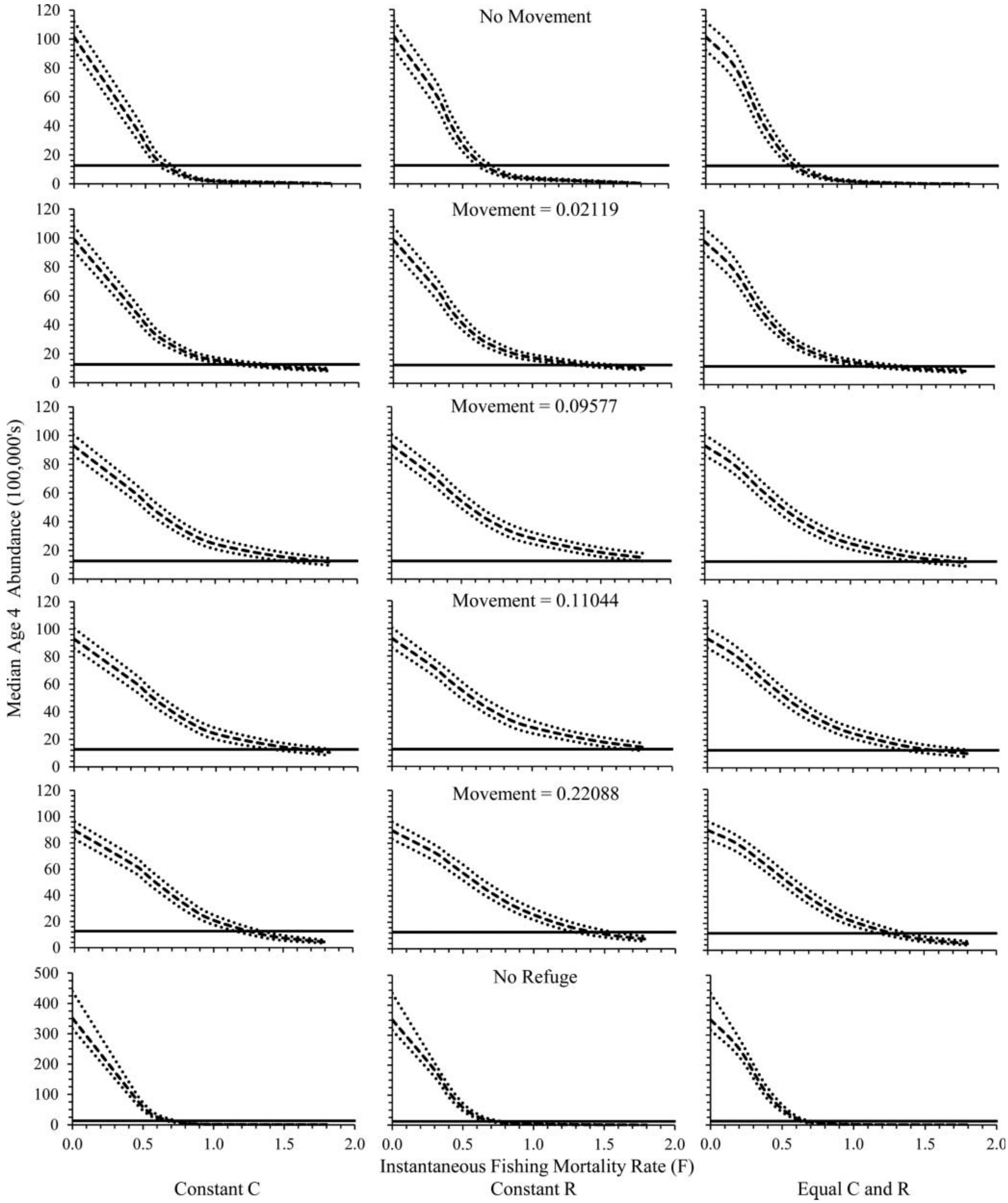

FIGURE 6. Median simulated abundance (±95% confidence interval) of age-4 Lake Trout versus the instantaneous fishing mortality rate (F) under varying movement rates and combinations of commercial (C) and recreational (R) fishing mortality in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration). The horizontal line depicts the reference for collapse (10% of the estimated Lake Trout abundance during 1980–2012).

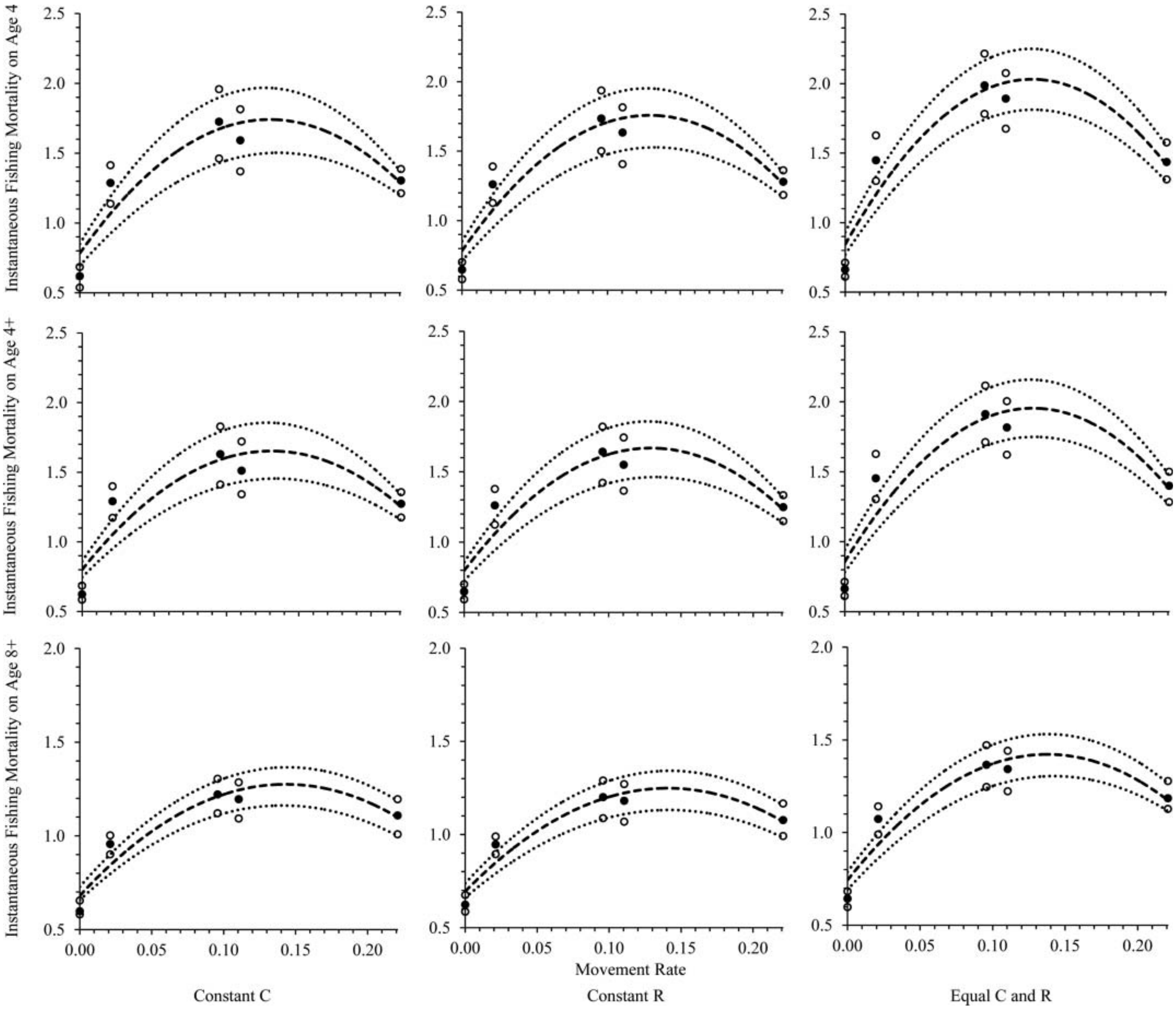

FIGURE 7. Instantaneous fishing mortality (F; ±95% confidence limits) of Lake Trout at collapse (<10% of 1980–2012 abundance) versus the movement rate under varying combinations of commercial (C) and recreational (R) fishing mortality for age-4, age-4 and older (age-4+), and age-8+ Lake Trout in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration).

collapse peaked at movement rates between 10% and 15% for both age-classes (Figure 11). Without the refuge, the probability of collapse increased from 0.0 to 1.0 for both fishable and adult Lake Trout at a lower F and at a faster rate (Figure 11).

When the movement rate was above zero, the refuge prevented the Lake Trout population from reaching extinction within 200 years, whereas removal of the refuge resulted in extinction within 200 years (Figure 12). When the refuge was maintained but the movement rate was zero, time to extinction began to decline below 200 years when F was 1.02 under equal levels of F_C and F_R; when F was 0.9 under a constant F_R; and when F was 1.0 under a constant F_C (Figure 12). In the absence of the refuge, time to extinction declined from 200 years to 80 years as F increased from 0.78 to 1.8 under a scenario of equal F_C and F_R; from 200 years to 147 years as F increased from 0.78 to 1.0 under a constant F_C; and from 200 years to 177 years as F increased from 0.86 to 1.0 under a constant F_R (Figure 12).

DISCUSSION

The Gull Island Shoal Refuge was most effective at protecting Lake Trout recruits (age 4) at the highest observed movement rate (11%) rather than the median observed (2%) or highest simulated (22%) movement rates. Similarly, studies of other refuges have shown that effectiveness is maximized

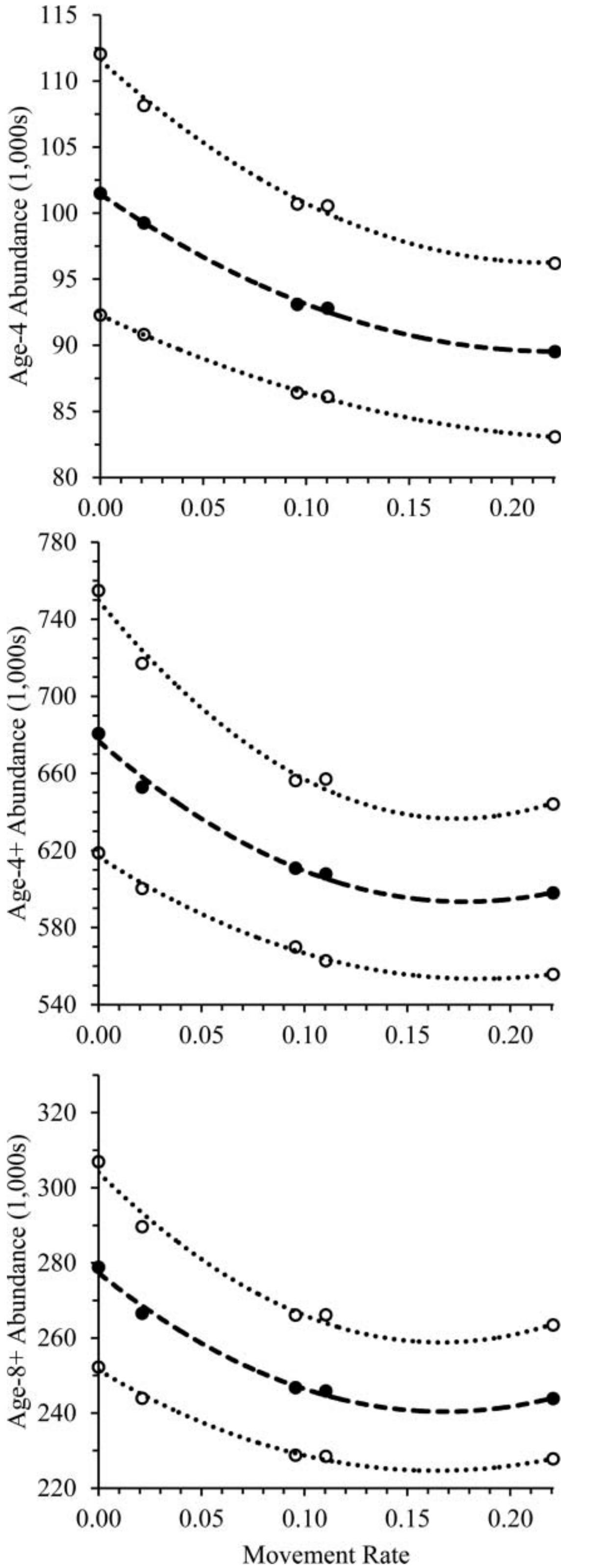

FIGURE 8. Abundance at an instantaneous fishing mortality rate (F) of 0 versus the movement rate of age-4, age-4 and older (age-4+), and age-8+ Lake Trout in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration).

when movement rates are neither too high nor too low to protect the population (Lindholm et al. 1998; Gerber et al. 2003; West et al. 2009). Furthermore, minimum refuge size is inversely related to movement rate, so larger refuges are needed to protect fish populations that move at higher rates (Gerber et al. 2003); this suggests that the Gull Island Shoal Refuge is large enough to support the median observed movement rate we evaluated. When the refuge was maintained, Lake Trout recruitment collapsed in our simulations when the movement rate was zero. As other studies have shown, providing recruitment to non-refuge waters is fundamental to a refuge's success, because the non-refuge population cannot be supplemented if there is no movement out of the refuge (Man et al. 1995; Lauck et al. 1998; Agardy 2000).

With continued use of the Gull Island Shoal Refuge, the abundance of fishable (age-4+) Lake Trout also remained sustainable at increasingly high levels of F and was best protected at intermediate movement rates (10–15%). Refuge removal induced the collapse of age-4+ Lake Trout at an F of 0.72 under all allocations of F_C and F_R; this F-value is higher than that reported for the Lake Trout population in Lake Pend Oreille, Idaho, which collapsed as F increased from 0.4 to 0.5 for gillnetting and from 0.6 to 0.7 for angling (Hansen 2007; Hansen et al. 2010). The difference between studies may be attributable to the fact that our results depicted only the fishable population outside the refuge. In a previous modeling study of Lake Trout in WI-2, Nieland et al. (2008) reported that the fishable stock collapsed when F was 0.41–1.40 depending on the mortality source, whereas our results showed that the mortality source did not greatly affect collapse. However, the selectivity curves for commercial and recreational fisheries were much more similar in our model than in the model used by Nieland et al. (2008), which may explain the difference in results.

Adult (age-8+) Lake Trout were sustainable when the refuge was maintained, but a fixed F_R induced collapse at a higher F than other combinations of fishing mortality, thus indicating that adults were less susceptible to varying levels of F_C than to varying levels of F_R, unlike the results of other modeling studies focused on Lake Trout in zone WI-2 (Nieland et al. 2008) and in Lake Pend Oreille (Hansen et al. 2010). Nieland et al. (2008) observed that adult Lake Trout declined more when F_R was held constant and F_C was varied. Similarly, Lake Trout in Lake Pend Oreille were suppressed more effectively by gillnetting than by angling (Hansen et al. 2010). In our simulations, when the refuge was maintained, adult Lake Trout collapsed at lower levels of F for all movement rates than did recruits (age 4) or the fishable stock (age 4+), suggesting that adults are more susceptible to fishing mortality than younger age-classes. Nieland et al. (2008) also showed that adult Lake Trout declined at lower F than the fishable stock, although the refuge was not included in that study. We found that when the refuge was removed, all three age-groups (age 4, age 4+, and age 8+) collapsed at similar

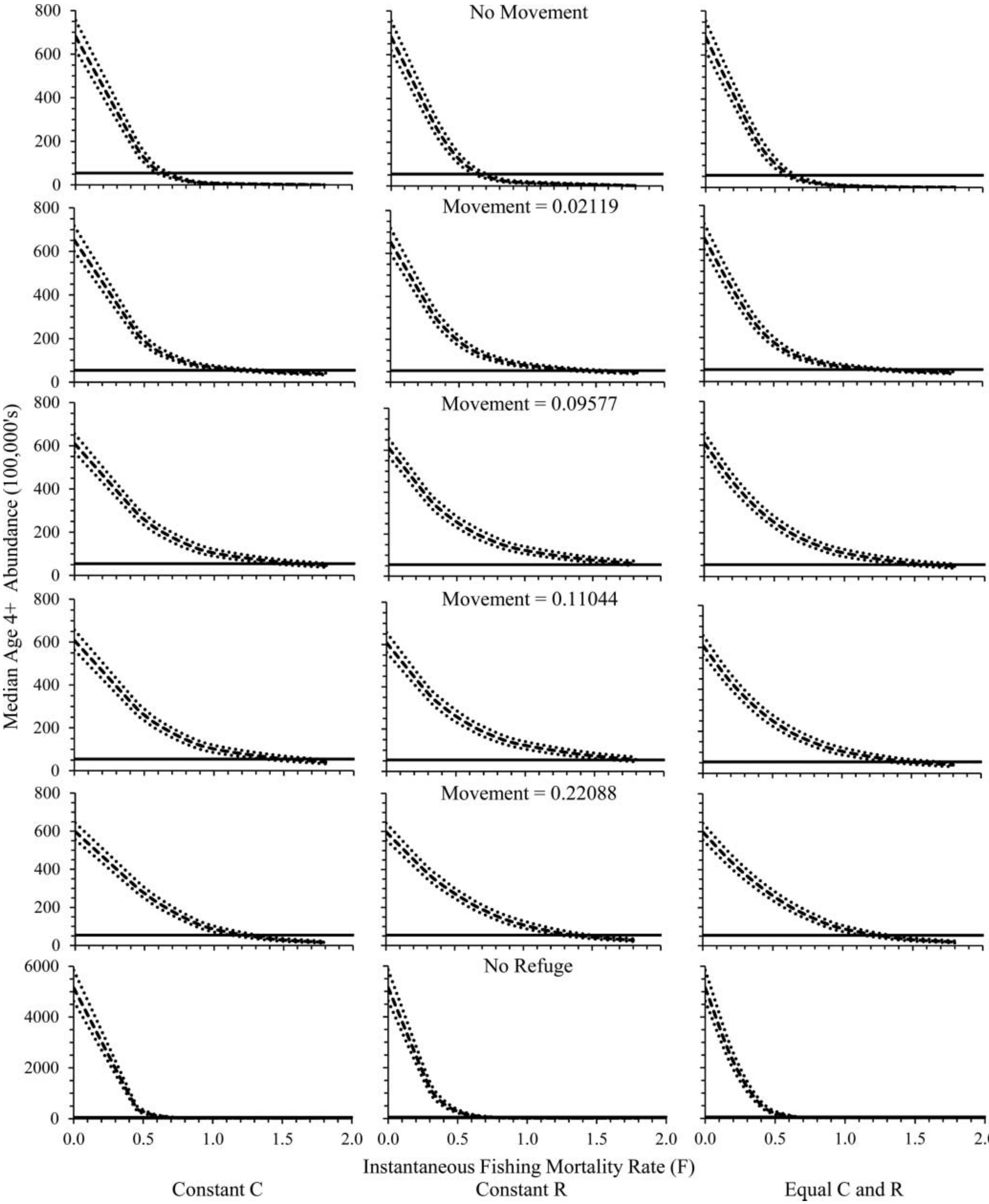

FIGURE 9. Median simulated abundance (±95% confidence interval) of age-4 and older (age-4+) Lake Trout versus the instantaneous fishing mortality rate (*F*) under varying movement rates and combinations of commercial (*C*) and recreational (*R*) fishing mortality in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration). The horizontal line depicts the reference for collapse (10% of the estimated Lake Trout abundance during 1980–2012).

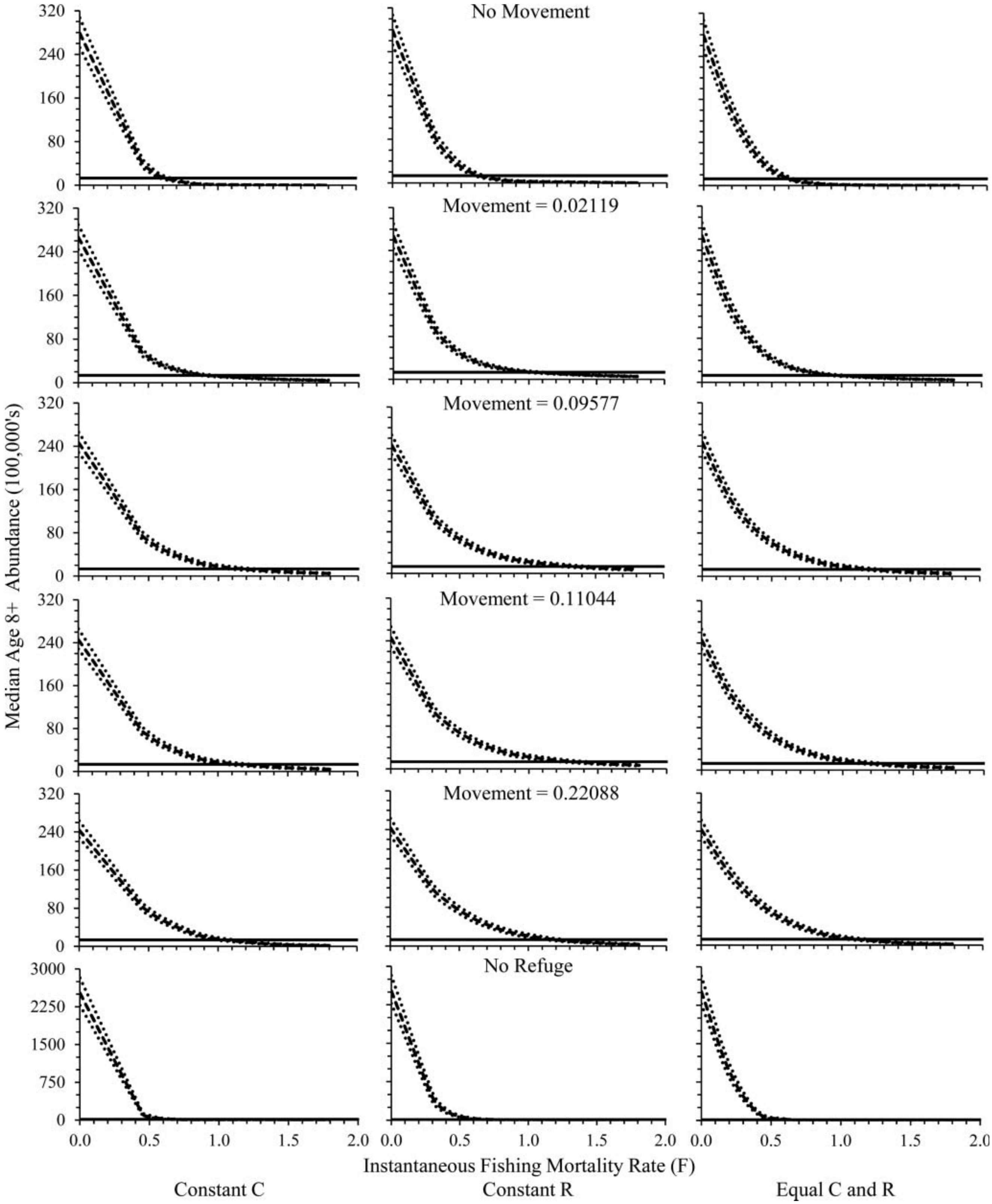

FIGURE 10. Median simulated abundance (±95% confidence interval) of age-8 and older (age-8+) Lake Trout versus the instantaneous fishing mortality rate (F) under varying movement rates and combinations of commercial (C) and recreational (R) fishing mortality in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration). The horizontal line depicts the reference for collapse (10% of the estimated Lake Trout abundance during 1980–2012).

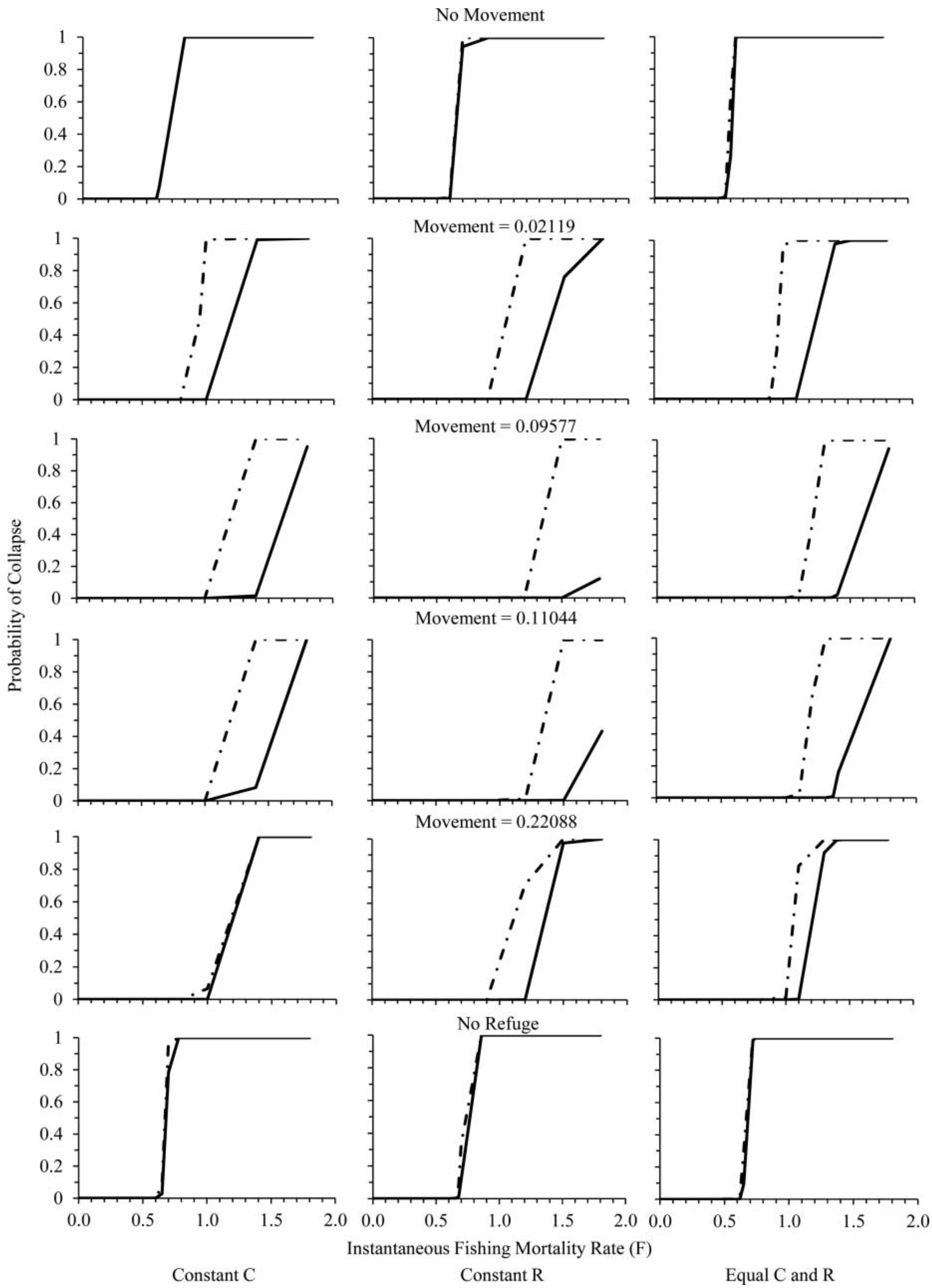

FIGURE 11. Probability of stock collapse versus the instantaneous fishing mortality rate (F) for age-4 and older (age-4+; solid line) and age-8+ (dashed line) Lake Trout under varying movement rates and combinations of commercial (C) and recreational (R) fishing mortality in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration).

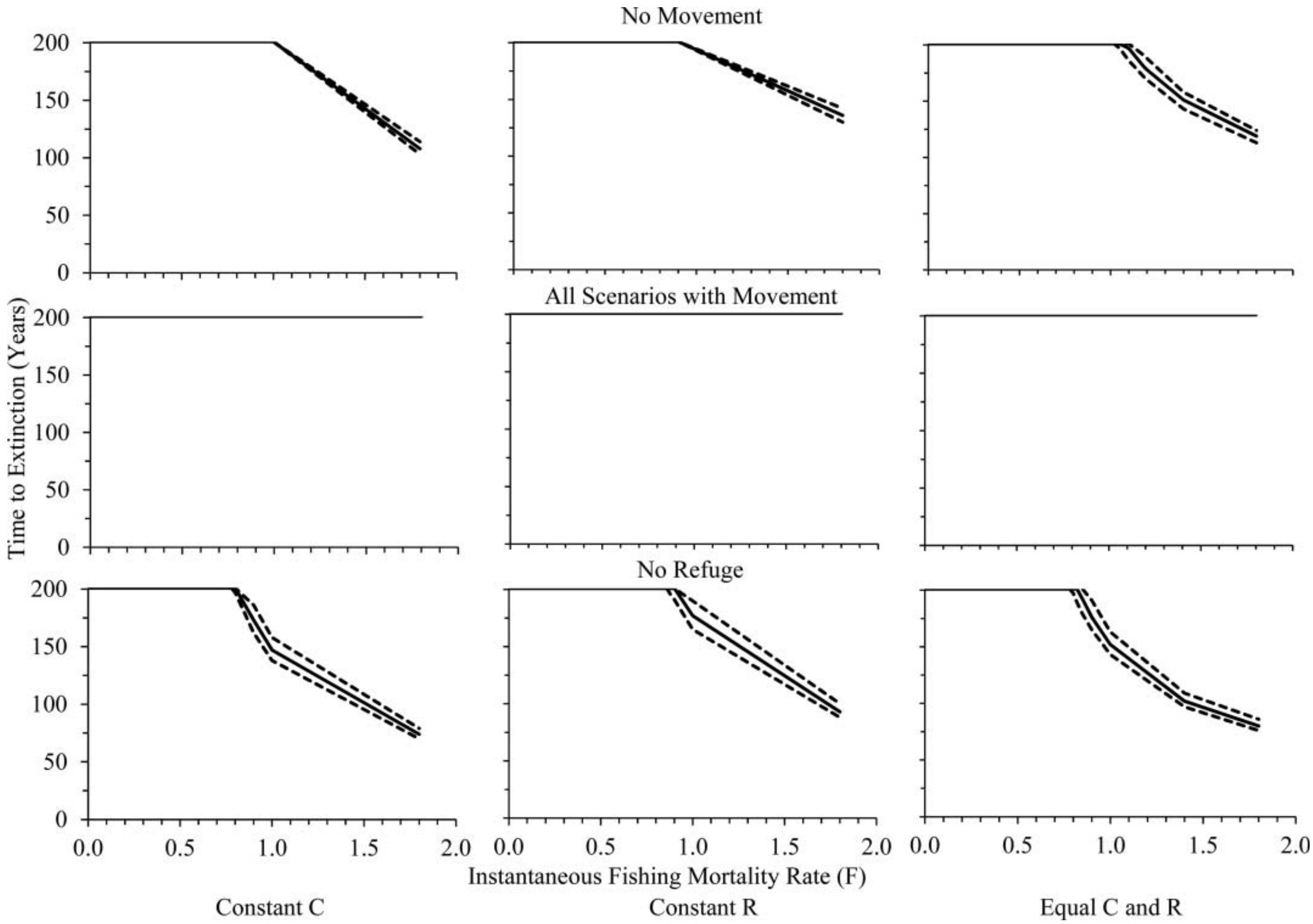

FIGURE 12. Time to extinction (±95% confidence interval) versus the instantaneous fishing mortality rate (*F*) for Lake Trout under varying movement rates and combinations of commercial (*C*) and recreational (*R*) fishing mortality in non-refuge areas within eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years/iteration).

F-values, unlike the results of the Nieland et al. (2008) study; a likely explanation for this difference is that the age-specific selectivity curves in our model were more similar than the age-specific selectivity curves in their model.

Collapse of fishable (age-4+) and adult (age-8+) Lake Trout was induced at higher *F*-values with the refuge than without the refuge, but adult abundance collapsed at a lower *F* than the fishable stock, which suggests that adults are more susceptible to fishing mortality than younger Lake Trout. Likewise, Nieland et al. (2008) showed that adult Lake Trout declined at a lower *F* than younger fish. The refuge was most effective in protecting fish at intermediate movement rates (10–15%). This accords with other refuge studies in which high movement rates were shown to be suboptimal because a refuge's effectiveness for protecting stocks from collapse generally decreases as movement increases, whereas fish with low movement rates rarely leave a refuge and therefore are rarely caught (DeMartini 1993; Gerber et al. 2003; West et al. 2009). Removal of a refuge thereby renders a population more vulnerable to collapse, as was observed for several species of large, predatory coral reef fish whose densities declined significantly after removal of no-take marine reserves (Russ and Alcala 2003).

We found that the refuge protected the Lake Trout population from going extinct within 200 years under all simulated levels of *F* except when the movement rate was zero. Similar findings were obtained from simulation of a marine reserve's effects on Mediterranean Hake *Merluccius merluccius*, which demonstrated that the reserve provided resilience because extinction was predicted at a much higher fishing mortality rate when a reserve was in place (Apostolaki et al. 2002). Spillover increases fishery yields, allowing a refuge to buffer against extinction due to fishing mortality; thus, in our simulations, the Lake Trout population's response to zero movement in the presence of the refuge was similar to that observed for removal of the refuge (Russ and Alcala 1996; McClanahan and Mangi 2000; Gerber et al. 2003). We found that time to extinction fell below 200 years at an *F* of 0.78–0.86 in the absence of the refuge, unlike Nieland's (2006) study of Lake Trout in WI-2 wherein time to extinction fell below 200 years at an F_C of 0.38 and an F_R of 0.49 (however, the Nieland 2006 model did not account for the refuge). We found that refuge removal caused extinction at lower levels of F than retention of the refuge, as in other cases of high extinction risk from fishing; a refuge provides recruits to overfished areas, thereby promoting a sustainable level of catch (Man et al. 1995; Gerber et al. 2003).

Our findings will aid fishery management in Wisconsin waters of Lake Superior in two ways. First, we found that the Gull Island Shoal Refuge would likely prevent Lake Trout stock collapse over a wide range of F-values, regardless of the manner in which F_C and F_R are allocated, thereby enabling fishery managers to sustain the stock regardless of fishery allocation. In contrast, if the refuge is removed, fishery managers will have to reduce F below current levels (i.e., through harvest or effort restrictions) to sustain the population. The refuge would protect the Lake Trout population from collapse regardless of such fishery management actions, as has been found for other fisheries (Quinn et al. 1993; Wallace 1998; Neubert 2003; Russ and Alcala 2003). Second, we found that the refuge afforded optimal protection at movement rates near the upper limit of the distribution estimated from mark–recapture, which provides assurance to fishery managers that the refuge is appropriately sized for the plausible range of movement rates between refuge and non-refuge waters within zone WI-2. Importantly, as Lake Trout density within the refuge increases toward carrying capacity of the area, fish movement from refuge to non-refuge waters will likely increase, thereby subjecting more Lake Trout to fishery exploitation. The Gull Island Shoal Refuge is sized appropriately for such higher movement rates.

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