Joint analysis of stressors and ecosystem services to enhance restoration effectiveness

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Edited by Peter M. Kareiva, The Nature Conservancy, Seattle, WA, and approved October 31, 2012 (received for review August 13, 2012)

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With increasing pressure placed on natural systems by growing human populations, both scientists and resource managers need a better understanding of the relationships between cumulative stress from human activities and valued ecosystem services. Societies often seek to mitigate threats to these services through large-scale, costly restoration projects, such as the over one billion dollar Great Lakes Restoration Initiative currently underway. To help inform these efforts, we merged high-resolution spatial analyses of environmental stressors with mapping of ecosystem services for all five Great Lakes. Cumulative ecosystem stress is highest in near-shore habitats, but also extends offshore in Lakes Erie, Ontario, and Michigan. Variation in cumulative stress is driven largely by spatial concordance among multiple stressors, indicating the importance of considering all stressors when planning restoration activities. In addition, highly stressed areas reflect numerous different combinations of stressors rather than a single suite of problems, suggesting that a detailed understanding of the stressors needing alleviation could improve restoration planning. We also find that many important areas for fisheries and recreation are subject to high stress, indicating that ecosystem degradation could be threatening key services. Current restoration efforts have targeted high-stress sites almost exclusively, but generally without knowledge of the full range of stressors affecting these locations or differences among sites in service provisioning. Our results demonstrate that joint spatial analysis of stressors and ecosystem services can provide a critical foundation for maximizing social and ecological benefits from restoration investments.

Laurentian Great Lakes | cumulative impact | marine spatial planning | fresh water

The Laurentian Great Lakes contain over 80% of North America's surface fresh water and are a critical resource to communities throughout the region (1). Lake-dependent commerce in US counties bordering the Lakes provided 1.5 million jobs generating US$62 billion in wages in 2010 (2). Economic activity associated with recreational fishing is estimated to be at least $7 billion annually (3), and millions of visitors swim, boat, and watch wildlife along the Lakes each year. Despite clear societal dependence on the Great Lakes, their condition continues to be degraded by numerous environmental stressors likely to have adverse impacts on species and ecosystems (4). As a result, water-quality advisories and beach closings are frequent occurrences, embodying both the human and natural costs of declines in ecosystem health (5).

Managing and restoring these high-value ecosystems has often been piecemeal, emphasizing one or a few stressors that garner public attention (e.g., an invasive species, nutrient run-off), or focusing on mitigation specific to a particular ecosystem service (e.g., fisheries management, recreational access) (e.g., ref. 6). Recent studies have demonstrated the value of more comprehensive assessments for prioritizing restoration investments, particularly when a broad suite of stressors or services can be quantified and mapped (7–10). However, to date the overlap and interaction between the cumulative impact of stressors and service provisioning has not been assessed in any ecosystem.

Restoration efforts explicitly merge concerns about stressors and services by seeking to reduce human impacts to increase provisioning of services. Since 2009, the Great Lakes have been the focus of a major restoration initiative entailing proposed expenditures of greater than $1 billion over 5 y by the US government (4), targeting invasive species, nonpoint run-off, chemical pollution, and habitat alteration. High return on this restoration investment is expected because of enhanced property values, reduced water treatment costs, and increased tourism, recreation, and fisheries (11). The current initiative specifically targets key classes of environmental stressors that were identified through a planning process involving numerous government agencies and environmental groups. However, despite the fact that both stressors and services occur in defined locations and vary greatly across space in magnitude, no comprehensive spatial analysis has been available to guide restoration efforts in the Great Lakes.

Quantifying and mapping the separate and cumulative influence of diverse stressors is an emerging new approach for optimizing restoration investments (7, 8, 12). The lack of comprehensive, spatially explicit stressor analyses raises at least three concerns. First, optimal targeting of restoration efforts often will require accounting for a wide range of stressors that differ in relative impact. Second, major investments in remediating a subset of stressors at

Author contributions: J.D.A., P.B.M., and B.S.H. designed research; J.D.A., P.B.M., S.D.P.S., B.S.H., G.L.B., A.B., G.A.B., L.M.C., W.L.C., J.J.H.C., P.J.D., T.E., D.M.I., L.B.J., C.A.J., A.L.M., A.P., J.G.R., J.B.R., E.S.R., S.P.S., and A.D.S. performed research; J.D.A., P.B.M., S.D.P.S., and B.S.H. analyzed data; and J.D.A., P.B.M., S.D.P.S., and B.S.H. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

Data deposition: The data reported in this paper are available at www.greatlakesmapping.org.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1213841110/-/DCSupplemental.

a site may have little net benefit if other stressors remain unaddressed. Finally, restoration planning is increasingly oriented toward maintaining or enhancing ecosystem services (13, 14), which requires identifying locations where actual or potential provision of services is greatest. Thus, understanding the spatial distributions of both stressors and ecosystem services can greatly enhance the strategic targeting of restoration efforts. Here we present a high-resolution assessment of cumulative stress (hereafter abbreviated CS) across the Great Lakes based on 34 stressors, ranging from fishing to land-based pollution to climate change (*SI Text*, Tables S1 and S2). These individual stressors represent all major classes of stressors in the region, and were weighted to reflect their relative impact on ecosystem condition. We then compare patterns of CS with the spatial distribution of seven ecosystem services related to food provisioning and recreational activities. Our results illustrate how joint analysis of stressors and services can be an important step toward maximizing social and ecological benefits from restoration investments.

Results and Discussion

Cumulative Stress Analysis. Our CS index highlights major spatial disparities in human influence across the Great Lakes (Fig. 1). Large subregions of moderate to high CS are apparent in Lakes Erie and Ontario, Saginaw and Green Bays, and along Lake Michigan's shoreline (Fig. 1). In contrast, extensive offshore areas of Lakes Superior and Huron, where the coasts are less populated and developed, experience relatively low stress (Fig. 2*A*). Although the median value of CS across the Lakes is 0.14 and <10% of pixels score above 0.3 (Fig. S1), most areas experience 10–15 stressors with nonzero levels (mean = 12.9 ± 2.6 SD, minimum = 8). Thus, a focus on one or a few stressors will miss the majority of the stressors affecting any given location. CS also differs strongly among habitats. The highest stress is seen in wetlands and river mouths, and CS declines rapidly from the shoreline to offshore (Fig. 2*B*). Near-shore habitats generally experience 12–18 stressors (mean = 15.2 ± 3.0 SD, maximum = 31), reflecting the coincidence of land- and lake-based stressors. This pattern is troubling from a biodiversity perspective, because roughly 90% of Great Lakes fish and invertebrate species occupy near-shore habitats (15).

Variation in CS is driven largely by concordant spatial patterns in multiple stressors, although few stressors are strongly correlated. Individual stressor intensities show broad positive correlations with CS across the Great Lakes, with the exception of copper contamination and climate-driven water warming (Fig. 3*A*). High CS results from above-average values of many different

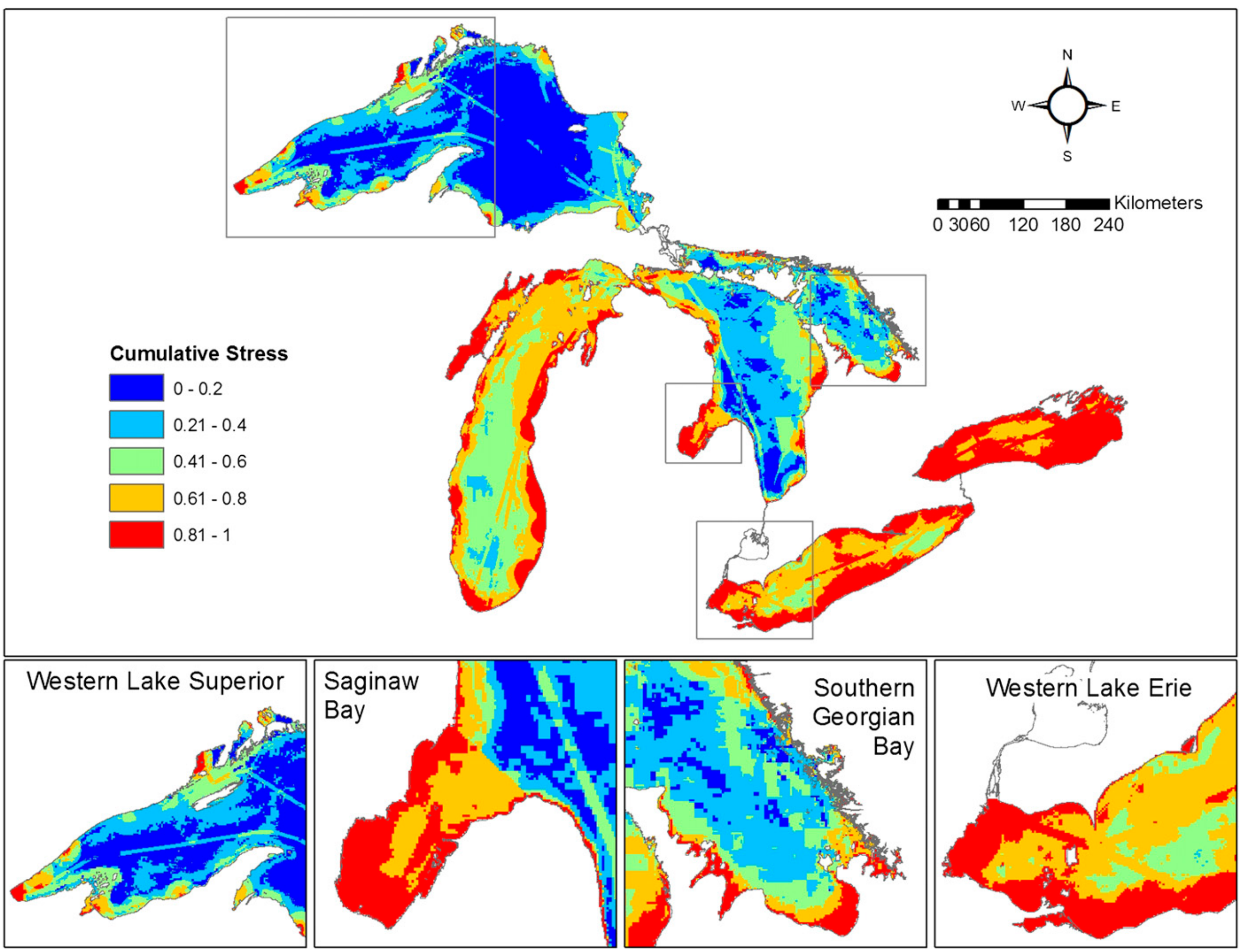

Fig. 1. The spatial pattern of CS from 34 human-induced stressors across the Laurentian Great Lakes and in selected regions. Cumulative stress was calculated based on the intensities of each stressor weighted by their impact (determined from expert judgment). We show CS on a relative (percentile) scale, grouped by quintiles; pixels representing the highest 20% CS are red, and the lowest 20% are dark blue. See Fig. S1 for the CS ranges of these quintiles.

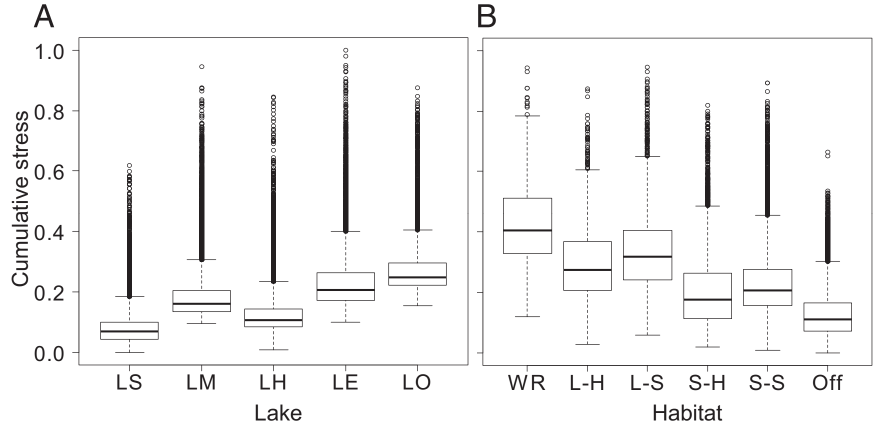

Fig. 2. Boxplots of cumulative stress for each lake (*A*) and habitat (*B*) in the Laurentian Great Lakes, showing medians and quartiles as boxes, 1.5× interquartile range as whiskers, and outliers as circles. Abbreviations used: Lakes Superior (LS), Michigan (LM), Huron (LH), Erie (LE), Ontario (LO); wetlands and river mouths (WR), littoral-hard substrate (L-H), littoral-soft substrate (L-S), sublittoral-hard substrate (S-H), sublittoral-soft substrate (S-S), offshore (Off).

classes of cooccurring stressors (Fig. 3*B*) rather than extreme values of any single stressor. Therefore, restoration efforts aimed at mitigating one or a few types of threats could fail to improve ecosystem conditions because of ongoing degradation from remaining stressors. Ideally, restoration planning should explicitly address multiple stressors and design interventions based on the relative impact of each stressor present at a site. Furthermore, high CS does not arise from a consistent suite of stressors. Instead, the lack of clustering of high-CS pixels in multivariate analyses of stressor intensities indicates that high stress results from a wide range of stressor combinations, although modest differences among lakes are evident (Fig. 3*C*). Sensitivity analyses show that spatial patterns of CS are robust to alternative stressor weights, normalization methods, and elimination of any particular stressor at both local and whole-basin scales (*SI Text*).

Interestingly, the spatial distribution of current restoration investments is focused almost entirely on high-stress locations. Among 33 long-standing areas of concern (AOCs), which are often associated with polluted rivers (16), and 231 georeferenced projects under the US Great Lakes Restoration Initiative (GLRI) (4), most are in the highest quintile of CS (Fig. 4 *A* and *B* and Fig. S2). This pattern presumably reflects the spatial correlation of most individual stressors with CS, including the stressors for which remediation is a priority under the AOC and GLRI programs. Although a focus on one or a few stressors may identify important locations to target, use of a more comprehensive, multistressor approach increases the likelihood that mitigation efforts will address all important stressors at a site.

Overlap of Ecosystem Services and CS. Comparing the spatial distributions of CS and ecosystem services reveals that locations supporting Great Lakes fisheries and recreation are disproportionately stressed (Fig. 4*C*). In particular, the locations of beaches, marinas, and perch spawning areas are strongly skewed toward high-CS areas. These patterns reflect broad north-south gradients in lake productivity and human population densities, both of which peak in Lakes Erie, Ontario, and southern Lake Michigan. Furthermore, high CS at bird-watching and charter fishing sites results from the concentration of human impacts along the shoreline and in wetlands and river mouths. In contrast, the skew in CS is lower for commercial fishing, which is widely distributed throughout all lakes, and lake trout spawning, which is concentrated in Lakes Michigan, Huron, and Superior, where average CS values are relatively low.

Interpretation of the spatial coincidence of CS and ecosystem services (Fig. 4*C*) depends on two assumptions: whether our multistressor index is an appropriate measure of stress to each service, and whether all service locations actually deliver benefits to people (i.e., have service value). We recognize that not all stressors affect a given service equally, so to test the first assumption we identified a subset of stressors expected to most directly and strongly influence each service. For example, we identified three stressors strongly affecting birding (light pollution, road density, and coastal development), and 10 stressors that have strong effects on commercial and recreational fishing (Table S3). Consistent with our analysis based on the full CS (Fig. 4*C*), services occur disproportionately in locations where the most relevant subset of stressors indicates high stress levels (Fig. 4*D*). As before, lake trout spawning and commercial fishing show the least departure from the null case where service locations are randomly distributed with respect to CS. For all services, departures from the null pattern are somewhat less pronounced when considering only the most relevant stressors, implying that mitigating a modest number of key stressors could result in measureable improvements in benefits.

For several services, including birding, beaches, and the two fish-spawning datasets, we did not have information on actual delivery of the service. Birding sites are a small subset of high-value sites identified by experts, or featured in birding festivals, so the assumption that they are visited seems reasonable. Beach visitation data are not available, but aerial views of beaches that had the fewest people living within a 30-km radius revealed campgrounds and road access for most, indicating that few if any beaches are unvisited. Spawning locations are compiled from historical data but are not individually monitored, so we must assume that all of them contribute similarly to the recruitment of these important fishery species.

In locations of high stress and low service provisioning, further investigations will be needed to ascertain whether services have always been low, or instead are currently suppressed by stressors. Only in the latter case is restoration likely to lead to improvements. Similarly, the cooccurrence of many service locations with high stress (Fig. 4 *C* and *D*) requires further research to determine if these services would benefit from restoration or are sufficiently resilient to stress that restoration is unnecessary. However, beach closings (17), sport fishery declines (18), and other types of foregone recreational opportunities suggest that stressor mitigation could indeed enhance service provisioning. For example, a number of studies have found that improvements in water quality result in increased benefits (19), consistent with estimates that Great Lakes restoration efforts could yield returns in excess of $50 billion beyond their costs (11). Although

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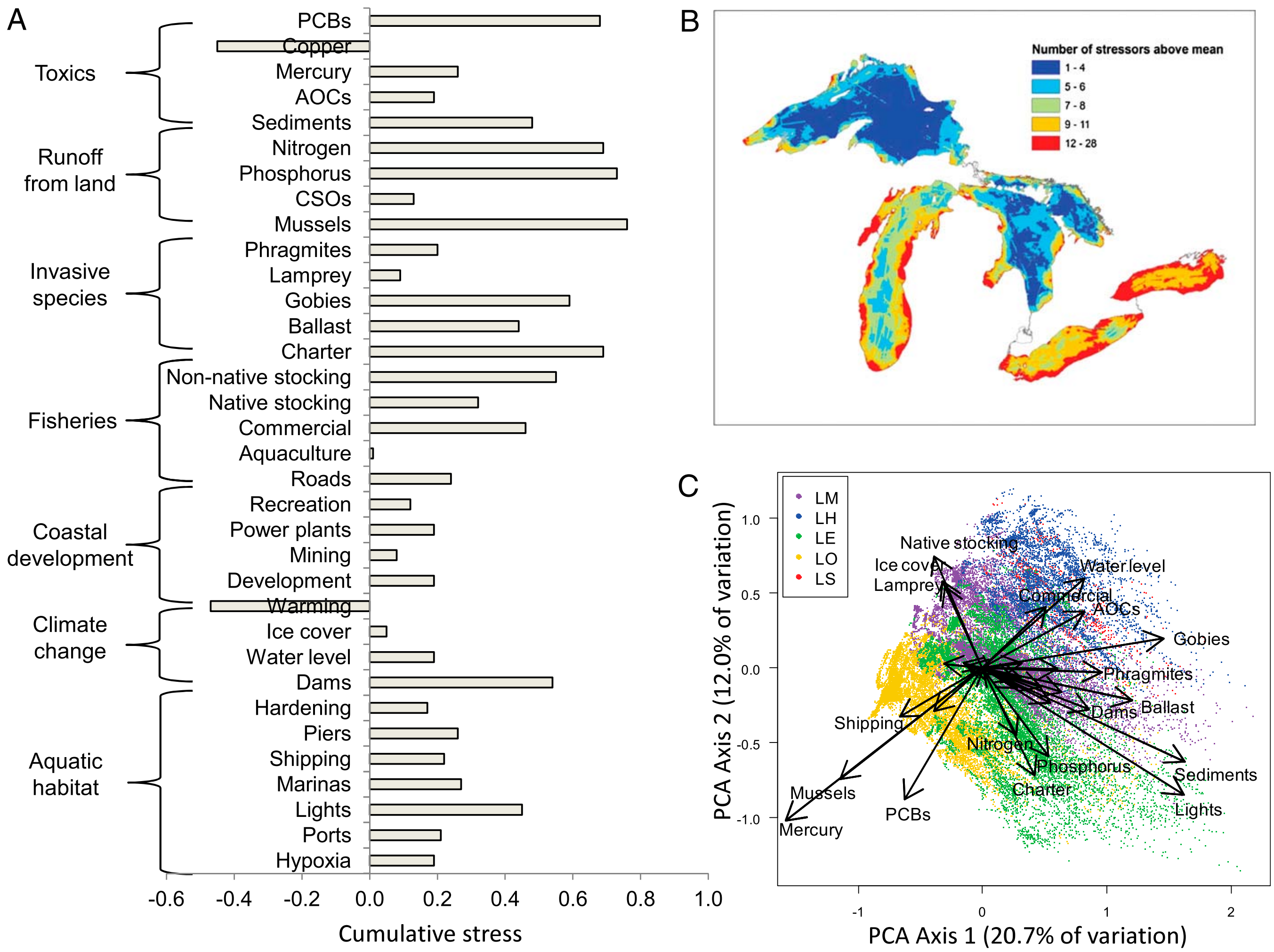

Fig. 3. Relationship between CS and individual stressor intensities in the Laurentian Great Lakes. (*A*) The correlation coefficient for each individual stressor map with the CS map, plotted as bars for better visualization. Because most stressors are positively correlated with CS (*A*), the number of stressors above their basin-wide average in each pixel (*B*) contributes strongly to variation in CS. However, unconstrained ordination of stressors in high-stress (CS > 0.8) pixels (*C*) failed to identify a consistent suite of operative stressors. The PCA biplot (*C*) shows factor loadings of stressors as arrows and site scores as points colored by lake (n = 47,899 pixels). See *SI Text* for descriptions of each stressor; lake abbreviations as in Fig. 2. CSOs, combined sewer overflows.

uncertainty remains about how decreases or increases in CS will translate into changes in particular services, there is reason for optimism that reducing ecosystem stress may provide tangible benefits to the region.

Restoration Opportunities

Our analysis highlights the potential to broaden the current portfolio of restoration projects by identifying locations of moderate-to-high CS that are not currently targeted for restoration, as well as sites not currently highly stressed that would benefit from mitigation of particular stressors. Particularly compelling opportunities arise when ecosystem services are high at sites where few stressors must be alleviated to significantly lower CS. For example, although most of Lake Ontario is in the highest quintile of CS, both the number of stressors to be alleviated (e.g., Fig. 3*B*) and levels of valued services vary widely among sites. The northeastern end of Lake Ontario exemplifies the opportunity to address multiple services by mitigating fewer stressors. At the other end of the CS spectrum, our approach enables identification of low-CS sites where services are high. These places may also offer high return on restoration investment because relatively few issues must be addressed and much service value could be lost if their CS levels were to increase.

Joint analysis of CS and ecosystem services also suggests that return on restoration investments may be low when high-CS sites require remediation of many stressors yet currently provide few services. Although our analysis focused on the limited set of services for which spatial data are available, it uncovered a number of current restoration project sites with high CS but low service provisioning. These locations would not be identified as high priorities based on a full analysis of stressors and services, although they may offer other benefits for which we have not accounted. Indeed, we advocate expanding the approach developed here to encompass additional value frameworks, such as protecting undeveloped areas or species and habitats of concern, and we recognize that restoration decisions must account for a variety of other factors such as economic costs, public perception, and equitable distribution of funding opportunities as well. Nevertheless, spatial analysis of both CS and ecosystem services provides a fresh perspective on prioritizing restoration sites and actions. Explicitly accounting for ecosystem services may also enhance the willingness of the public and policy-makers to support restoration efforts.

Conclusions

Given the large number of individual stressors included and the robustness of our results in sensitivity analyses (Table S1, Fig. S3),

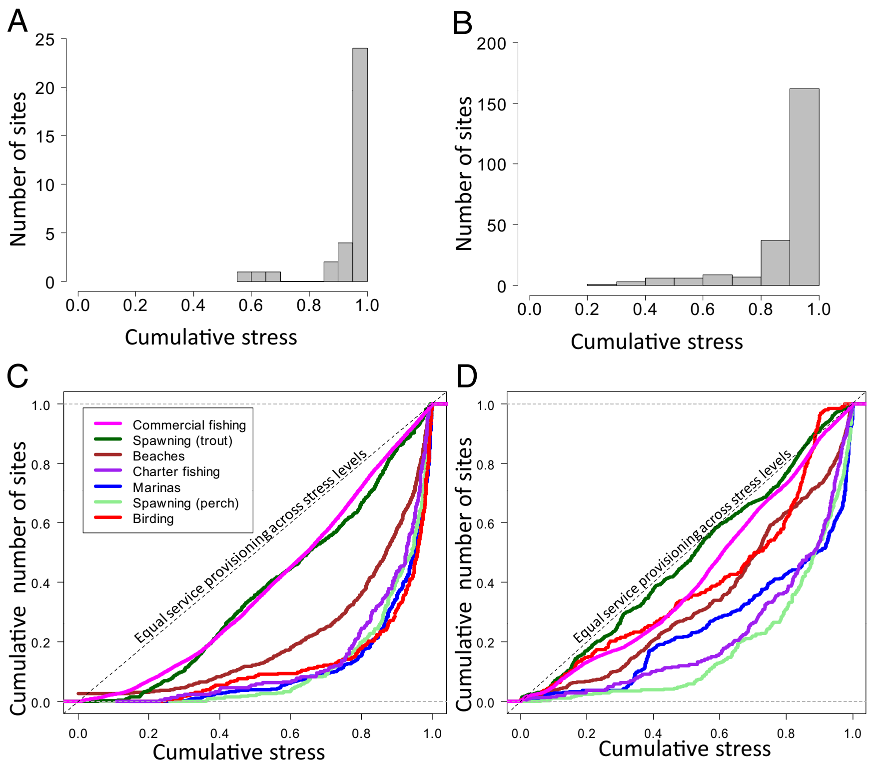

Fig. 4. Locations of current restoration efforts and valued ecosystem services coincide with areas of high CS in the Laurentian Great Lakes. Histograms of the frequency of CS at 33 AOC (*A*) and 231 GLRI sites (*B*) show that these sites are predominantly in locations with high CS. (*C*) The cumulative frequency of CS in locations of seven ecosystem services (sample sizes: beaches, 1,265; marinas, 445; birding, 297; charter fishing, 240; lake trout spawning, 1,143; yellow perch spawning, 336). Each curve shows the proportion of sites at or below a given CS. All curves fall below the 1:1 line, indicating that these services occur in areas of higher CS than expected at random. (*D*) The cumulative frequency of stress in locations of the same seven ecosystem services, where stress is estimated using the most relevant subset of stressors specific to each service.

the patterns of ecosystem degradation revealed by our CS index across the 244,000 km^2 of Great Lakes waters are unlikely to change with additional information. Nonetheless, interpretation of our results must recognize several limitations. We used a 1-km^2 grid to resolve shoreline features, but variation in the native scale of data and assumptions of stressor decay with distance from input sources make our results most useful for identifying broad-scale patterns. The spatial distributions of some important stressors could not be quantified, including additional invasive and nuisance species, recreational fishing, fish diseases, and emerging toxic chemicals. Our CS index is additive because interactions among stressors (20, 21) and nonlinear impacts on ecosystems are poorly understood. For example, apex predators in Lake Huron have collapsed following dreissenid mussel invasion (22), but this synergy cannot yet be predicted. Future assessments of ecosystem services would benefit from comparative valuation data and from direct evidence of service response to stressor mitigation, both of which are major gaps in current understanding of the Great Lakes and other ecosystems. Finally, economic costs and political constraints strongly influence real-world restoration decisions (12, 14), but are beyond the scope of our analysis.

Enormous societal investments in restoration of the Great Lakes and other critical ecosystems are underway, providing high-profile tests of our ability to improve ecosystem conditions and human well-being. Prioritizing on-the-ground actions within these efforts is challenging when dozens of stressors are in play and their relative importance varies in space. High-resolution spatial analysis is an effective approach for assessing human impact on ecosystems at global (7, 8) to regional (23) scales, and can assist restoration efforts by identifying the full range of stressors that degrade ecosystem condition at any given site. Here, we extend this approach to account for ecosystem services and place current restoration efforts in a multistressor context. Our results show that additional restoration investments in the Great Lakes are warranted, and provide a means of targeting them at the stressors and sites where societal and ecological benefits would be maximized.

Materials and Methods

We assembled data for 34 stressors likely to have adverse impacts on species, biological communities, or ecosystem dynamics across the entire surface of the Great Lakes, excluding connecting channels (*SI Text*). Stressors were mapped at a 1-km^2 resolution to adequately represent shoreline and bathymetric features of the lakes. Datasets used to generate individual maps differed in their native resolution (Table S2), and we used standard geospatial methods for resampling and interpolation to convert them to a common grid (*SI Text*). When original dataset extents did not align with our template because of boundary inconsistencies, small gaps with no data values near the shoreline were filled in by interpolation.

We modeled the spatial footprint of stressors with influence beyond their point of origin (e.g., sediment loads entering a lake from a river) in two ways (*SI Text*). For stressors from tributary inputs, we modeled dispersal over distance from the river mouth into the lake using an exponential decay function with stressor-specific coefficients. For shore-based stressors, we assumed that influence extended 1 km into the lake and transferred the shore-side stressor value to the adjacent lake-side pixel. Although stressor decay estimates are uncertain, we have used reasonable estimates based on the literature and consultations with subject-area experts. To account for the differential vulnerability of various habitats to each threat, we developed a habitat classification based on bathymetry, substrate composition, and the locations of wetlands and river mouths (Fig. S4). We combined wetlands and river mouths because many important wetlands within the Great Lakes are associated with river mouths and to simplify the number of categories needed for an expert survey. Using expert elicitation methods

(24), we distilled survey responses from Great Lakes experts into quantitative weightings of the relative impact of each stressor on ecosystem condition for each lake and habitat type (*SI Text*). Respondents were asked to consider each stressor independently, and to not attempt to account for interactions among stressors or generalizations about differential occurrence of each stressor. The resulting weights for the 34 stressors pooled across habitats ranged from 1.82–4.02 as proportional contributions to CS (Table S1). Although surely imperfect, these weightings represent the synthesis of expert opinion and are likely superior to the alternative assumption that all stressors have equal impact.

The ln[$x + 1$]-transformed value of each stressor's intensity was multiplied by its relative weight, pixel by pixel, and CS was computed additively as the sum of the weighted stressors (8):

$$CS = \sum_{i=1}^{n} S_i * \mu_{i,j}, \qquad [1]$$

where S_i is the normalized stressor value at location i and $\mu_{i,j}$ is the weight of stressor i in ecosystem zone j, with n = 34 stressors and where j is one of 30 ecosystem zones (five lakes by six habitats). To examine the robustness of our results, we performed a variety of sensitivity analyses addressing both procedural issues and data limitations. All sensitivity analyses were executed at the pixel scale, and included tests of how spatial patterns of CS are affected by different algorithms for standardizing data to a 0–1 scale, applying equal or randomized weightings of stressors, and eliminating individual stressors to mimic changes in data availability. Full details and analytic results are presented in *SI Text* .

Ecosystem services were mapped by synthesizing data on human uses of the lakes that are directly linked to commerce and rely on the health of the Great Lakes, including three recreational uses (beaches, marinas, and bird-watching areas), two provisioning services (commercial and charter fishing), and spawning areas for two important fishery species (lake trout and yellow perch) (Fig. S5). We then constructed cumulative frequency curves for each service ranked by ascending CS to explore whether service locations would be equally common across all levels of stress (Fig. 4*C*, 1:1 line) or deviate toward under- or overrepresentation. When the service was also used in CS, we used CS recalculated for the other 33 stressors.

Of the 39 current AOCs, we identified 33 that were located along the Great Lakes shoreline or a major Great Lakes tributary (16). We computed average CS for the aerial extent of the AOC or for a 5-km radius around its river mouth when an AOC did not extend into the lake. Of the > 600 GLRI projects funded in 2010 and 2011 (4), we identified 231 active restoration projects as affecting the Lakes based on their reported project descriptions, primary focus areas, and locations. Most projects involved restoration activities in the lakes themselves or within 10-km inland of the shoreline. We also included GLRI projects >10 km from the shoreline if they addressed a stressor directly affecting the lakes (including nutrient or sediment delivery from inland locations and AOCs); we mapped these projects to the downstream river mouth of the watershed. We analyzed CS for the water pixel adjacent to the project location. We computed the empirical distribution function in R (25) to create cumulative frequency curves, showing the total number of projects with scores at or below a given CS.

To explore whether particular combinations of stressors characterized areas of high stress, we performed multivariate analyses of ln[x + 1]-transformed stressor intensities within high-stress areas (CS > 0.8, n = 47,899 pixels). To examine whether a small number of groups captured the variation in stressor intensities, we performed K-means nonhierarchical cluster analysis with 1–20 clusters. To understand whether particular sets of stressors varied together (which would also indicate discrete sets of stressors leading to high CS values), we performed principal components analysis (Fig. S6).

See *SI Text* for more detailed information on data sources, methods, and analyses. Individual stressor maps can be viewed at www.snre.umich.edu/gleam/allan_pnas_appendix2.

ACKNOWLEDGMENTS. We thank P. Esselman, L. Mason, F. Yousef, R. Biel, J. Fenner, K. Hanson, and J. Olson for assistance with stressor mapping; R. Cooke for weighting analysis; R. Hecky for contributing to project development; M. Carlson-Mazur, A. Fusaro, K. Kowalski, D. Jude, H. MacIsaac, N. Mandrak, T. Nalepa, D. Reid, A. Ricciardi, C. Riseng, and R. Sturtevant for guidance on invasive species; S. Carpenter, S. Januchowski-Hartley, and M. Moore for comments on the project; and scientists at numerous universities and agencies for sharing stressor data. Comments by reviewers added significantly to the analysis. This project was funded by the Fred A. and Barbara M. Erb Family Foundation; The Nature Conservancy's Great Lakes Fund for Partnership in Conservation Science and Economics (W.L.C., P.J.D., and S.P.S.); and the University of Wisconsin-Madison (P.B.M.).

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Supporting Information

Allan et al. 10.1073/pnas.1213841110

SI Materials and Methods

Stressor List and Weightings. We use the term "stressor" to refer to a physical, chemical, or biological factor that potentially has adverse effects on ecosystem condition. We focus on stress rather than condition per se because the quantitative conversion of stressor levels into specific impacts on condition is difficult to achieve at the ecosystem level. However, previous comparisons of multivariate stress scores to ecosystem condition in the world's oceans (1) and Great Lakes watersheds (2) suggest that the types of human modification included in this study do indeed translate into real-world impacts.

During a series of expert workshops, we developed a list of 50 anthropogenic stressors affecting the Great Lakes (Table S1). Criteria guiding stressor selection were: (*i*) stressors result in some alteration of the biology, chemistry or physical structure of the Great Lakes ecosystem and its catchment, (*ii*) stressors represent a distinct mechanism of impact, and (*iii*) stressors had potential availability of spatial data encompassing all five lakes. We excluded stressors with incomplete coverage because this could bias basin-wide spatial comparisons. Sufficient data were available to create basin-wide maps for 34 stressors. We group the stressors into seven higher-level categories: aquatic habitat alteration, climate change, coastal development, fisheries, invasive species, nonpoint pollution, and toxic chemicals. We did not include municipal water withdrawals because quantitative spatial data are not available. Detailed methods are provided for individual stressors in *Environmental Stressors*, below, and spatial data sources are documented in Table S2.

We used an expert survey modeled after a published example from marine ecosystems (3) to derive weightings that reflect relative risk of ecological impact. The survey assessed the vulnerability of each lake and habitat type to each stressor on the basis of five components of ecosystem impact. We received responses on the ecosystem ratings portion of the survey from a total of 161 Great Lakes researchers and natural resource managers. The survey results were used to derive a single integrative weight for each stressor on a 0–1 scale based on accepted decision science methodologies (3). These quantitative weightings (pooled weights in Table S1) enabled us to account for disparities in the ecological impact of different stressors in different habitats of different lakes. For example, the expert consensus was that high levels of certain invasive species can generate over twice as much stress as high levels of coastal recreation in the near-shore zone of Lake Michigan. Thus, these weightings allow cumulative stress (CS) to be calculated in an additive way by converting heterogeneous stressor intensity values into a common currency of expected impact on ecosystems. Survey respondents rated each stressor independently of other stressors; we did not attempt to account for interactions among stressors or nonlinear impacts of stressor intensity. Our survey yielded a synthesis of expert opinion about the relative impact of different stressors.

Our survey required respondents to consider each stressor independently of others, which may lead to imperfect rankings; nonetheless, equal weighting of stressors is clearly incorrect, and the methods we used have been validated elsewhere (3). In addition, sensitivity analyses show our results are robust to such potential differences.

Data Representation and Projection. All data, regardless of native resolution, were mapped to a common resolution of 1-by-1 km using a grid imposed within a modified Albers Equal-Area coordinate system. The customized coordinate system has parameters defined based on the extent of the watersheds of the Great Lakes (extents: N: 50.738281° N; S: 40.399673° N; W: 93.205208° W; E: 74.499374° W). Parameters for this coordinate system are: Central Meridian 84.455955° W; Parallel 1 42.122774° N; Parallel 2 49.015180° N; Latitude of Origin 45.568977° N; False Easting 1,000,000 m; and False Northing 1,000,000 m.

Stressor Mapping. All stressors were mapped across the five Great Lakes, excluding connecting waters (St. Mary's River, St. Clair River, Lake St. Clair, Detroit River, Niagara River), and terminating at the St. Lawrence River outlet of Lake Ontario. Datasets used to generate individual maps differed in their native resolution, and we used standard geospatial methods for resampling and interpolation to convert them to a common grid (Table S2). We selected a 1-km^2 grid cell to adequately represent near-shore contours and bathymetric features of the lakes, resulting in 243,937 pixels. When original dataset extents did not align with our template because of boundary inconsistencies, small gaps with no data values near the shoreline were filled in with interpolated data values for continuous data or nearest-neighbor values for categorical data. Specific data transformations are described in sections that document individual stressors; here we provide a brief summary. For stressor datasets with a native scale coarser than 1 km^2, the value from the original dataset was assigned to each receiving cell, distributing the value equally across the full area within the original cells. Examples include fish stocking, commercial fish harvest, summer warming, and ice cover. Five data layers were interpolated from point data observed at coarser scales using standard methods of geospatial statistics, specifically kriging. This process includes dissolved oxygen (for hypoxia), dreissenid mussels, and the three toxic data layers, each of which was represented by an extensive sampling grid. The remaining stressor datasets were at the kilometer or subkilometer scale.

For stressors whose influence extends beyond their point of origin (e.g., sediment loads entering a lake from a river mouth, shoreline modification affecting the near-shore zone), we modeled the spatial extent and used the modeled stressor levels for all subsequent calculations. For several stressors associated with onshore development (e.g., road density, shoreline hardening) we conservatively assigned the value of a shore pixel to the adjacent water pixel, assuming that intensity of influence would be negligible beyond 1 km. For other stressors we assumed a greater dispersal distance represented by a 2D exponential decay function. Coefficients were selected to represent the distance at which the intensity of a stressor's influence was expected to decay to 10% of initial value, where it would be difficult to distinguish stressor influence from background. That distance was 2–5 km for most coastal stressors (e.g., contaminants associated with sewer outfalls, mining, power plants, marina activities, commercial ports). Model coefficients were chosen based on published studies of distance effects (e.g., near-shore mine waste distribution) or other evidence of distance of impact (e.g., length of power plant water intake pipes) or by pairing with a better evidenced stressor likely to have similar effects. River-exported sediments and nutrients were expected to disperse to greater distance (decay to 10% of initial value in 10–15 km) as evidenced by satellite imagery of river plumes and limited lake survey data. Stocked fish and young sea lampreys emerging from natal streams were assigned greater dispersal distances (50–150 km) based on literature reports and expert judgment. For some human activities (recreational boating, charter fishing) we consulted marina managers and charter captains for estimates of distance traveled. Further explanation of decay distance is provided with each stressor description.

Dispersal modeled as 2D exponential decay results in successive concentric rings and undoubtedly fails to take into account complexities of currents and mixing, fish dispersal, and human behavior. We acknowledge this limitation, but it was infeasible to develop more comprehensive models for all stressors across all lakes; in addition, data to validate more detailed models are largely lacking. Further investigation of the influence of materials and activities extending from land to near-shore and then to offshore across a range of environmental conditions is an urgent need.

The final step in our standardization of stressor maps was to express every stressor variable on a uniform numeric scale. Before transformation, distributions of each stressor differed, but most were skewed to the right or zero inflated. Following Halpern et al. (1), values in each cell were $\ln[x + 1]$-transformed, then rescaled from 0 (zero or minimum observed value) to 1 (maximum observed value) (using max-min rescaling: $[x_i - x_{min}]/[x_{max} - x_{min}]$). This continuous, unitless scale allows direct comparison of stressors whose native units vary widely.

Sensitivity Tests of Calculation Methods. Our analysis required a variety of decisions about computational procedures, each of which could have influenced our conclusions. To verify that our analyses were robust to alternative procedures, stressor weightings, and data availability, we tested the sensitivity of our results to permutations of each type. Our interpretation of these sensitivity tests focused on the robustness of spatial patterns in the CS index, because those patterns are the basis for our key inferences. However, all sensitivity tests were executed at the pixel scale, thereby elucidating responses to computational permutations at both the basin-wide and pixel-specific spatial scales across the Great Lakes.

Sensitivity to data standardization. Our CS calculations required merging stressors, the native units of which vary widely. Rescaling the pixel values of each individual stressor to a 0–1 range served this purpose by creating a unitless, relative metric of the intensity of a given stressor at a particular location. Similarly, rescaling our CS index to a 0–1 range facilitated interpretation by creating an intuitive range of values. Therefore, for both individual stressors and the CS index, we considered three types of transformations to accomplish the 0–1 standardization. First, we used a basic max-min linear rescaling ($[x_i - x_{min}]/[x_{max} - x_{min}]$). Second, we used a natural-log transformation ($\ln[x + 1]$) before max-min rescaling, thereby compressing the upper end and expanding the lower end of the range. This process had the effect of minimizing the influence of extremely high values that could be spurious yet influential, and it is common practice in studies of ecological impact of stressors (1). Third, we used a cumulative distribution function (CDF) to replace each stressor or CS value with a score reflecting its percentile rank relative to all other pixels (4). The CDF approach resulted in a uniform number of pixels at any given level of stress, whereas the linear and log transformations allowed heterogeneity in the number of pixels at any given level of stress.

We applied all three transformation approaches separately to both the individual stressors and CS index. Each one yielded a range of scores from 0 (low stress) to 1 (high stress), and the spatial correlations were high among the resulting nine maps (based on all 36 pair-wise comparisons, Pearson's r: mean = 0.859, range 0.691–0.988). Thus, we conclude that our key inferences about spatial patterns of CS were independent of the normalization method for stressors and CS. For all analyses presented in the article, we used the natural-log transformation of stressor values followed by max-min linear rescaling of CS. This decision is in keeping with many previous studies on individual stressors, and using simple linear rescaling of the CS index retained all quantitative spatial information about variation in CS. However, we used the CDF transformation of the CS index in two places for graphical purposes. To simplify interpretation of the overall CS map, we present the results in Fig. 1 using a CDF transformation of the CS index, because the flat frequency distribution of CS scores across pixels facilitates visualization of broad spatial patterns in our results. We also used the CDF-transformed CS index to display the relationship between the location of ecosystem services and CS (Fig. 3); using CDF-transformed values enabled us to use the 1:1 line in the plot as a straightforward null-expectation, reflecting services being distributed randomly with respect to CS (Fig. 4). Nonetheless, our sensitivity tests showed that both broad patterns and pixel-specific results were affected very little by the choice of transformation approach.

Sensitivity to weightings. Our CS index combined the spatial data on individual stressors with the relative weights of those stressors derived from our state-of-the-art survey of Great Lakes experts (Table S1). Although we adopted a robust approach to deriving these quantitative weightings (following ref. 3), it is important to assess how strongly they affected the overall patterns of CS reported. To test the sensitivity of our CS results to the weightings, we compared two alternative approaches to our expert-derived weightings. First, we set all weights to 0.0294, representing a null-weighting model where every stressor contributes equally to CS. Second, we randomly shuffled the expert-derived weights 10,000 times, and recalculated CS for each set of permuted weightings.

We found that spatial patterns of CS are robust to alternative weightings. Expert-derived and null (equal) weightings produced CS results that were highly correlated across the entire Great Lakes (Spearman rank correlation = 0.995) (Fig. S3 *A* and *B*). To visualize the differences at a local scale, we quantified the difference in CS arising from null-weightings compared with our expert weightings. Minor differences were evident in some near-shore zones and in the paths of shipping lanes (which received a low stressor weight from Great Lakes experts) (Fig. S3*C*). However, no pixel exhibited a shift in pixel CS by more than 0.19 on the 0–1 scale, confirming that our analysis was robust at local scales as well as basin-wide. Similarly, CS from permuted weightings was closely correlated with CS from the original expert-derived weightings (Pearson's r: mean = 0.833, range 0.362–0.956, n = 10,000 permutations) (Fig. S3*D*). These high correlations between results from expert-derived, null, and randomized weightings demonstrate that the weightings had only a modest influence on CS at any spatial scale.

Sensitivity to stressor data inclusion. Although we accounted for a more exhaustive set of stressors than most previous large-scale analyses of CS, it remains possible that our results could have been disproportionately influenced by spatial patterns in only a few stressors, or that accounting for an additional stressor could have changed the overall pattern. We tested these possibilities by quantifying the influence of individual stressors using a jackknife-style sensitivity test. For each of our 34 stressors in turn, we set its weighting to 0.0 and adjusted all other weightings proportionately upward so that the remaining 33 stressor weightings still summed to 1.0. CS was recalculated for each 33-stressor set, and the correlation between CS scores from the 34- and 33-stressor results was calculated across all pixels. At the pixel scale, we also evaluated the range of CS values that arose from exclusion of a single stressor.

We found that spatial patterns of CS were robust to exclusion of any single stressor. Results were strongly correlated in every case (Pearson's r: mean = 0.995, range 0.972–1.000) (Fig. S3*E*); therefore, no one stressor had substantial influence. Rather, the patterns of CS revealed by our analysis reflect broad patterns in the spatial distribution of many stressors. This result was also true at the scale of individual pixels; the maximum effect of eliminating one stressor from the CS calculation was a change of 0.07 on the 0–1 scale. By extension, this sensitivity test indicates that our overall CS results would be unlikely to change if one or a few additional stressors were accounted for in the analysis as further data become available, even if these new stressors showed substantially different spatial patterns than any current stressor in our analysis.

Conclusions from sensitivity tests. Careful tests of the sensitivity of the CS index to shifts in data transformations, stressor weightings, and inclusion of specific stressors all indicate that our CS results were robust. At the basin-wide scale, there were strong spatial correlations between our original results and each permutation. These tests give us confidence that the spatial patterns of CS shown in Fig. 1 are robust. Thus, even if one or a few of our stressor maps were poor representations of actual spatial patterns, this would have negligible effects on the overall pattern of anthropogenic stress across the Great Lakes. Results would also have been comparable with alternative transformation approaches or stressor weightings.

At the local scale of interest to many managers and restoration ecologists, our CS index also proved robust. Although the emphasis of our analysis was large-scale patterns derived from high-resolution data, our sensitivity analyses were rooted in pixel-scale permutations. Altering the transformations, weightings, and stressor data used generally caused only small (usually <10%) changes in CS for individual pixels. Thus, the fine-scale patterns emerging from our CS analysis are reasonable representations of the available data on stressors across the Great Lakes. However, we caution against overinterpreting pixel-scale values as statements of current environmental quality at specific locations; that is not the intent of our analysis, and at present we are unable to validate our CS index against equally high-resolution field data on actual environmental quality.

SI Ecosystem Units

Habitat Categorization. To allow comparisons across habitats, we developed a simple six-category classification based on bathymetry, substrate type, and the locations of wetlands and river mouths. Water depth was used to establish three zones: littoral (0–5 m), sublittoral (5–30 m), and offshore (>30 m). The 5-m contour separating the littoral and sublittoral is intended to account for differences in light penetration and influence of wave action. The thermocline maximum depth is ∼25–30 m in late summer, functionally distinguishing near shore from offshore conditions. Because Lake Erie is shallower and has a distinct, three-basin structure, its depth zones were set at 0–3 m, 3–15 m, and >15 m. Substrate information was obtained from a variety of sources (5–14) and was integrated into a composite map. Initially, substrate was classified from native dataset categories into hard, sand, clay, and mud, and subsequently reclassified into hard vs. soft (sand, clay, and mud). Finally, because wetlands and river mouths are of particular importance, their presence or absence was used as a third characteristic. River mouths are the major conduit of land-based stressors into the lakes, pathways for potadromous fishes, and significant locations of human commerce and recreation. Wetlands are important as nursery ground for many taxa, and for nutrient cycling. We combined river mouths with wetlands to reduce the number of habitat categories needed for the expert survey to derive stressor weightings, and because many important wetlands within the Great Lakes occur naturally at river mouths. Each pixel was assigned to only one habitat type, such that a single habitat-specific weight was applicable to each stressor in a given pixel in the CS calculations.

The resulting habitat classification (Fig. S4) includes six categories: (*i*) wetland or river mouth, (*ii*) littoral-hard substrate, (*iii*) littoral-soft substrate, (*iv*) sublittoral-hard substrate, (*v*) sublittoral soft substrate, and (*vi*) offshore-pelagic. Gaps in data coverage for substrate forced us to add littoral-unknown substrate and sublittoral-unknown substrate in some areas (3.6% of total lake area). For weighting stressors in these areas, we used the average of the weightings from hard and soft substrate classes in that depth zone.

SI Environmental Stressors

Individual stressor maps may be found at http://www.snre.umich.edu/gleam/allan_pnas_appendix2. Data can be viewed at our project website, www.greatlakesmapping.org. Most data processing was done in ArcGIS (Esri).

Category: Aquatic Habitat Alterations. Aquatic habitat alterations were characterized with eight data layers, including hypoxia, light pollution, shipping lanes, ports, shoreline hardening, shoreline extensions, marinas, and tributary dams.

Hypoxia. Hypoxia, commonly defined as dissolved oxygen levels (DO) at or below the 2–4 $mg{\cdot}L^{-1}$ range, occurs in the bottom layer (hypolimnion) of some highly productive regions of the Great Lakes. Hypoxia usually occurs during late summer because of the decomposition of organic matter leading to oxygen depletion. Human-induced nutrient enrichment, particularly from elevated phosphorus inputs, has increased the frequency and areal extent of hypoxia. Because DO > 4 $mg{\cdot}L^{-1}$ is unlikely to be stressful to the majority of species (15), we estimated relative stress caused by hypoxia using the continuous range of DO values and a scale from 1 (no stress, >4 $mg{\cdot}L^{-1}$) to 0 (maximum stress, 0 $mg{\cdot}L^{-1}$). We mapped DO data for Lake Erie from September 2005 and Green Bay for September 2010. We also examined data for Saginaw Bay but found it did not meet our criteria for hypoxia. Point data were kriged to develop a continuous surface using ArcGIS algorithms with a neighborhood of five datapoints.

Light pollution. Light pollution because of human activity is especially pronounced in near-shore areas of high population density. Possible effects on aquatic organisms include disruption of fish foraging and reproductive behavior, and of vertical migration by zooplankton (a phenomenon in which zooplankton such as small crustaceans migrate to shallow waters by night to feed on algae and retreat to deeper waters during the day to avoid visually feeding fish). We extracted the data layer for light pollution ("Lights at Night", 30 arc seconds resolution), from the National Oceanic and Atmospheric Administration (NOAA) National Geophysical Data Center (NGDC) Web site. The data were resampled to conform to the project 1-km^2 grid. The data file represents a cloud-free composite made with Defense Meteorological Satellite Program Operational Linescan System data. This data source shows a decline in light intensity with increasing distance from light sources and results in near-total light attenuation by about 45-km offshore.

Industrial ports and harbors. Industrial ports and harbors concentrate shipping and other industrial activities in river mouths and embayments, with associated increased risk of physical habitat disturbance and pollution. Shipping within the Great Lakes involves as much as 200 million tons of cargo at more than 100 ports; primary cargos include iron ore, coal, limestone, and grain (16). We mapped the average number of ship arrivals at Great Lakes ports from 2007 to 2009, using port locations provided by the Great Lakes Maritime Research Institute (17) and ship arrival data from Bailey et al. (18). The most highly visited ports in this analysis include Duluth-Superior (MN-WI), Detroit (MI), Hamilton (ON, Canada), Toledo (OH), and Cleveland (OH). Because the impacts of port and harbor locations likely are restricted to the port vicinity, we assumed their influence decayed to 10% of effect within 2.5 km and was negligible at 5 km.

Shipping lanes. Great Lakes ports and harbors are connected by a complex network of shipping lanes, locks, and navigation channels that allow ships to travel over 3,000 km from Duluth, MN, to the Atlantic Ocean. Environmental impacts associated with shipping lanes include shoreline erosion from wave action caused by passing ships, substrate disturbance because of propeller wash in shallow areas, habitat degradation from ice-breaking and winter navigation, and pollution from ship discharges. We obtained shipping lanes data developed by the US Army Corps of Engineers (19), port locations from the Great Lakes Maritime Research Institute (17), and international shipping route data for1996–2000 from Colautti et al. (20). To estimate traffic by route, we recorded the first, second, and third ports of call for each ship, and summed the number of ships traveling between each pair of ports. We used the network analyst tool in ArcGIS to identify 1,369 potential shipping routes between port pairs, of which 281 were used by the international ships in our dataset. We assumed ships traveled using the shortest route. The most-traveled routes by all international ships included the east-west routes through Lake Ontario and Lake Erie and the north-south route in western Lake Huron. The most common trips originated in Thunder Bay (ON, Canada), Duluth-Superior (MN-WI), and Hamilton (ON, Canada), and were bound for overseas ports. Great Lakes navigation routes correspond to nautical charts published by the Department of Commerce, NOAA, and the National Ocean Survey and recommended to commercial shippers operating in the Great Lakes (21). We added a 2.5-km buffer to each side of the shipping channel to account for variation in route fidelity, wake effects, and ship discharges.

Tributary dams. The installation and management of dams threatens the diversity of native Great Lakes fish by restricting or eliminating connectivity between the lakes and critical spawning, nursery, and overwintering habitats (22–24). Tributaries also provide water, nutrients, and sediment to the Great Lakes, particularly to coastal and near-shore ecosystems (25). Although limitation of fish passage and denial of fish access to the upper watershed are important consequences of dams, these influences are difficult to quantify and so the influence of tributary dams as a stressor is limited in this analysis to those effects associated with altered delivery of sediments, nutrients, and organic matter. Dam data for Ontario were acquired from the Ontario Ministry of Natural Resources (OMNR). US dam data were derived from the National Anthropogenic Barrier Dataset developed through a project sponsored by the US Fish and Wildlife Service. At least 12,000 dams occur throughout Great Lakes basin; of these, ~3,400 are considered "large" (>2 m in height), including1,910 in Canada and 1,452 in the United States. This reduced list of dams >2 m is considered most likely to influence nutrient and sediment regimes via impoundments. The influence of watershed dams as a stressor was estimated using river tributaries as pour points, and the magnitude of the influence at the pour point was scaled to the count of dams per watershed. The influence of dams was then propagated into the Lakes assuming their influence decayed to 10% of effect within 15 km and became negligible at 30 km, identical to nitrogen and phosphorus propagation.

Shoreline hardening. Hardened shoreline has the potential to alter near shore sediment dynamics and accelerate lakebed erosion (26, 27). Shoreline hardening may facilitate establishment of lithophilic nuisance species like zebra and quagga mussels, and thus possibly aid the expansion of nuisance species throughout the Lakes (28). Lake Erie and its connecting waters have a very high extent of hardening, Lakes Michigan and Ontario are intermediate, and Lakes Huron and Superior have little shoreline hardening (29). Data for the United States and Canada were taken from the digital medium-resolution vector shoreline data set from the US Army Corps of Engineers and Water Issues Division of Environment Canada, Ontario Region. The shoreline protection classification portion of the dataset represents the extent to which individual segments of the shoreline are protected, noting the estimated percent of a respective reach that is protected structurally. We assume that the influence of shoreline hardening does not extend beyond 1 km into the lakes, and so the value for the shoreline pixel was then assigned to the adjacent water pixel.

Shoreline extensions. Groins, jetties, docks, and offshore breakwaters extend perpendicularly to the shoreline or are located offshore, and add another dimension to shoreline alteration. Such structures intercept and divert along-shore transport of sediments, potentially causing accumulation of sediments on the updrift side and sediment starvation on the down-drift side (30, 31). We inventoried Great Lakes shoreline structures along ~86% of the Great Lakes' 17,000 km of shoreline for docks using very high-resolution imagery (<1 m resolution) from multiple sources, with image-capture dates ranging from 2000 to 2010. For the US shoreline, the primary imagery source was 2008–2010 US Department of Agriculture National Agricultural Imagery Program imagery. For the Canadian shoreline, the primary imagery source was Google Earth supplemented with Bing Maps. The total number of large shoreline extensions was summed in each water pixel adjacent to shoreline. Groins have been reported to affect down-drift nearshore bathymetry for a distance of four times the groin length for individual groins and six times the groin length for a groin field (30). Because some structures extended as far as 0.5 km into the lakes, we applied a 2-km buffer to limit the overall effect of shoreline extensions to a distance of 2 km from the shore.

Marinas and recreational boating. Marinas are a potential source of chemical pollution because of boat maintenance activities and spillage of a variety of compounds (32), and may exert physical effects on the environment associated with boat wakes (33), harbor dredging, breakwaters, and shoreline structures (28). Marina locations were identified from internet sites and the number of boat slips was obtained from marina Web sites when available or were counted using aerial images. Marinas located within river-inland lake complexes were included if within 5 km of a Great Lake. We identified 726 marinas grouped into 504 locations around the Great Lakes, with an estimated 102,251 marina slips. Based on the finding that 93% of boat slips in marinas with zip codes that border the Great Lakes were occupied in 2004 (34), the estimated number of boats docked in marinas on the Great Lakes is 95,093. Studies cited above do not estimate distance of influence but we expect chemical pollution and physical disturbance to have only local effects. The influence of marinas was scaled the count of boat slips and assumed to dissipate to 10% of their initial value within 2.5 km and to 1% within 5 km.

Category: Climate Change. Climate change is assessed with three stressor layers: water level change, summer temperature, and winter ice cover.

Changing water levels. Great Lakes water levels have been relatively stable over the past 150 y, with only a 2-m difference between the recorded maximum monthly mean and the minimum monthly mean. Seasonally the lakes vary by 0.40–0.45 m (35). However, the Lakes have experienced considerable water level fluctuations in the past three decades relative to the 2-m range, with extreme high water in the 1970s to 1990s. Lake levels dramatically declined between 1997 and 2000, and are now near their recorded low. Shallow, near-shore regions of the lakes, including wetlands and river mouths, are particularly vulnerable to declines in water levels, which may result in increased demand for dredging. Although short-term lake level fluctuations can be beneficial to wetland biodiversity (36), prolonged change is likely to cause zonation shifts (37, 38), the consequences of which will depend in part on lake bathymetry. We assess water level as a stressor to the Great Lakes using the 3-m bathymetric contour. Although future changes may be less than 3 m, these shallow areas are expected to be most affected. Compilation of new bathymetry for the Great Lakes was carried out cooperatively between NOAA

(NGDC and the Great Lakes Environmental Research Laboratory), and the Canadian Hydrographic Service. Datasets from individual lakes were joined and resampled to conform to the project 1-km^2 grid. Where data gaps occurred near the shoreline, pixel values were populated with kriged data. Bathymetry pixels with depths <3 m are considered sensitive to climate change.

Warming summer temperatures. Summer surface-water temperatures appear to be increasing across the Great Lakes basin, with greater increases in the upper relative to the lower Great Lakes. Moreover, summer water temperatures appear to be warming at a faster rate than mean annual air temperatures in the upper Great Lakes (39, 40), evidently because of an earlier onset of summer stratification, which may last longer and become established at shallower depths. Model projections indicate surface temperature warming between 2000 and 2100 ranging from 0.37 to 0.93 °C per decade in Lake Superior to between 0.20 and 0.60 °C per decade in Lake Erie (41). Temperature changes will affect the metabolism of ectothermic organisms, alter the ranges and abundances of many species because of changes in thermal habitat, affect the timing of seasonal events, such as spring blooms of algae, and promote the spread of nuisance algae and invasive species. Some changes may be beneficial, however, as warmer temperatures likely will increase ecosystem productivity unless nutrients or other factors become limiting, and may expand the thermal habitat available to some native fishes. Daytime sea-surface temperature data from advanced very high-resolution radiometer satellite imagery were obtained from the NOAA CoastWatch program for the warmest three summer months (July 1 to September 30) in 1994–2010. We computed annual mean temperatures for each 3 × 3-km pixel during this 3-mo window. To calculate a water warming index, we used linear regression with least-squares fitting (regressing average temperature vs. year) and resampled estimated coefficients to the 1-km^2 grid. The slope of this regression represents the average temperature increase per year during the warm period of the year.

Reduced duration of winter ice cover. Changes in winter ice cover may influence lake levels via evaporative water loss and lead to higher water temperatures by affecting the onset of summer warming. Although the duration of winter ice cover has unquestionably decreased over the past century at locations including Grand Traverse Bay, MI (42), and Lake Superior in the vicinity of Bayfield, WI (43), trends across the surface of the Great Lakes are more complex. One measure, the annual maximum percentage of lake surface covered by ice, is highest in Lake Erie, despite having the fewest freezing degree days, because of its shallow mean depth (19 m); Lake Superior ranks second, because its high freezing degree days offset its greater mean depth (148 m). Relative ranking for the five Great Lakes also has changed across decades (44, 45). Although further analysis is needed, evidence to date and future projections suggest reductions in ice cover extent and duration characteristic of mild past winters, and Lakes Erie and Superior may show the greatest response (45). Ice cover data were obtained from NOAA's Great Lakes Ice Atlas (mostly the National Ice Cover dataset, but Canadian Ice Service data were used for dates when National Ice Cover data were not available). These data consisted of total concentrations (fraction of surface area covered) of ice across the Great Lakes basin, observed or interpolated daily in 2.5 × 2.5-km pixels throughout the winter (December 1–May 31) (44). We considered a pixel on a given day to be ice-covered if its area occupied by ice was ≥50%. For each winter from 1973 to 2002, the cumulative duration of ice cover (number of days having ice cover ≥50%) was calculated. Because the data in many pixels were not normally distributed, to determine whether there was a significant decrease in ice cover in a given pixel, Kendall's τ and P values were calculated using the nonparametric (rank-based) Mann–Kendall test (46, 47). For pixels that exhibited a significant decrease in ice cover (defined as Mann–Kendall $P < 0.10$ and trend direction negative), we expressed the rate of change in duration (i.e., days of ice duration lost per year) using the slope from simple linear regression, and resampled estimated coefficients to the 1-km^2 grid.

Category: Coastal Development. Coastal development was represented with five data layers: developed land, road density, mining, thermoelectric power plants, and coastal recreational use.

Developed land. Coastal development disrupts physical and hydrodynamic processes and generates pollutants that, because of lake proximity, may introduce diverse contaminants into near shore waters. US data were derived from the National Land Cover Dataset, a land cover classification that was derived from Landsat Enhanced Thematic Mapper+ (ETM+) satellite data. Canadian data were from the Ontario Provincial Land Cover Database, derived from Landsat-7 Thematic Mapper satellite data frames recorded between 1986 and 1997, most from the early 1990s. The extent of developed land including "settlement and developed land" in Canada and "developed" land in the United States was estimated by determining the percentage of developed land within a 5-km radius of each pixel within 1 km of the shoreline. We assume that the influence of developed land does not extend beyond 1 km into the lakes, and so the value for the shoreline pixel was then assigned to the adjacent water pixel.

Coastal road density. Roads are considered a distinct stressor because they provide access to the lakeshore, including in less-developed areas. Roads add to impervious surface area and alter the physical and chemical environment by contributing run-off polluted with road surface materials (48, 49). Coastal road density was derived from the Ontario Road Network 2005 on the Canadian side and TIGER/Line files from the US Census Bureau on the US side of the basin. We attempted to extract comparable data by emphasizing paved roads; identification of unpaved roads was not consistent between the metadata descriptions of the two data sources. In Canada, all surface roads of the surface type "paved" were included. For the United States, the following feature types were included: primary road, secondary road, local neighborhood road, rural road, city street, ramp, service drive, and parking lot road. We assume that the influence of roads also does not extend beyond 1 km into the lakes, and so the value for the shoreline pixel was then assigned to the adjacent water pixel.

Mining. Mining has the potential to introduce contaminants into lake waters and sediments, with documented impacts on aquatic life (50). We combine active and historic metal mines because of the potentially long legacy effect and often lesser regulatory restriction on historic metal mines. We also include limestone/dolomite mines, even though chemical leaching is not expected to be serious, because of the land disturbance associated with these mining operations and the large footprint of some mines. Calcite Quarry located in Rogers City, MI, on the shore of Lake Huron is the world's largest limestone mine. Quarries for excavating sand, gravel, and stones make up the vast majority of mines in the Great Lakes region, but they are not considered as a stressor here because they are unlikely to result in significant disturbance or contamination. Mine data comes from the US Geological Survey (USGS) Mineral Resources Data System (51) and the OMNR's Mineral Deposit Inventory. We consider all metal mines (historic and active) and active limestone/dolomite mines within 2 km of the shoreline of the Great Lakes to be potential sources of contaminants. Mines are not differentiated by size or likely impact because of lack of necessary data. Dispersal distance likely varies with type of material and coastal energy and currents. In addition, the signature of legacy mining has had many years to disperse. Studies document a steep drop in mine wastes away from shoreline locations of mining in the Great Lakes and note that high copper and mercury concentrations can be traced back to shoreline stamp mills and smelters

(52–54). Coarse sands from century-old copper mining along southern Lake Superior are concentrated within a few kilometers or less of shore, and a well-documented metal-rich "halo" extends tens of kilometers surrounding the Keweenaw Peninsula. We conservatively propagate the influence of mines assuming a decline to 10% of its initial value within 5 km and 1% within 10 km, and acknowledge that distances may substantially increase over time.

Thermoelectric power plants. Thermoelectric power generation from coal, oil, natural gas, nuclear, and biomass energy sources is the largest use of water in the Great Lakes basin (72% of all water use in 2005), with the majority of water used for plant cooling (55). Water intakes directly harm fish populations by impingement on water-intake screens and entrainment when smaller fish passing through screens are harmed by contact with infrastructure or by heat shock. Our analysis includes 114 coastal power plants located within 2 km of the Great Lakes shoreline on the assumption that these plants draw water directly from the Lakes or from major tributaries just upstream of their confluence with the Lakes. Because the size of a power station and the volume of water withdrawn are correlated (56, 57), we used power generation capacity to differentiate among power plants in size and presumed impact. Power plant data comes from the Emissions and Generation Resource Integrated Database, Statistics Canada, and the Ventyx Energy Velocity Map. Cooling water-intake locations can be as much as 500–1,000 m offshore, suggesting that impingement and entrainment of fish can encompass an area of at least 1 km and possibly more. Reported fish kills can be very large: the Bay Shore plant in Toledo, OH reported losses of 46 million adult fish impinged, and 14 million juvenile and 2 billion larval fish entrained (58). New York's Dunkirk Generating Station on the shores of Lake Erie and Huntley Generating Station on the Niagara River reported annual losses of 63 million adult fish and 97 million adult fish, respectively, because of impingement (59). We assumed that the influence of water withdrawals would decay to 10% of its initial value within 3.5 km and be negligible beyond 7 km.

Coastal recreational use. Great Lakes beaches are areas of high recreational use, hosting an estimated 8 million annual visitors (60). Recreational beach use may act as a stressor because of refuse from millions of visitors, foot and vehicle traffic in sensitive dune areas, and through beach maintenance activities, including beach grooming and infrastructure to reduce erosion. We mapped beaches as point locations along the shoreline. US beach locations were derived from the US Environmental Protection Agency (US EPA) Beaches Environmental Assessment and Coastal Health (BEACH) Act geospatial database. US beaches were represented by line segments, which we converted to points using the midpoint. The locations of Canadian beaches were provided by Environment Canada, and a small number of additional beaches were identified from protected lands databases for the United States and Canada. The stressor layer is based on the locations of 1,265 beaches. Because recreational impacts from beach visits are expected to be local and minor, we applied a 1-km buffer to all beach locations to estimate the lake area impacted by beach use.

Category: Fisheries. Under the broad category of fisheries-related stressors to the Great Lakes we recognize five individual stressors of potential importance: commercial fishing, recreational fishing, aquaculture, native fish stocking, and nonnative fish stocking.

Commercial fishing. Commercial fishing in the Great Lakes has experienced dramatic changes in target species and harvests because of the combined influences of overfishing, invasive species, and environmental deterioration (61, 62). Lake Erie supports the largest and most heavily managed commercial fisheries, focused on yellow perch and walleye, and has seen recent recovery of its lake whitefish fishery. Current fisheries emphasize yellow perch and lake whitefish in Lake Ontario; lake whitefish, walleye, and yellow perch in areas of Lakes Huron and Michigan; and cisco, lake trout, and lake whitefish in Lake Superior. Commercial fishing data were obtained from the USGS Great Lakes Science Center and from the OMNR. Commercial catch data were recorded in round pounds at a spatial resolution of 5-min grid cell for Canada and 10-min grid cell for the United States. The exceptions were the Canadian waters of Lake Ontario, where data are recorded at a much coarser "quota zone," and the US waters of Lake Ontario, where no spatial information was associated with the data. Data for the US waters of Lake Ontario were distributed to a relatively confined area (Chaumont Bay) with a smaller amount being distributed near Fox and Grenadier Islands based on communications with OMNR biologists. Finally, the data were down-scaled assuming equal distribution of harvest within each reporting unit across our 1-km pixels, using the cubic convolution algorithm in ArcGIS.

Recreational fishing. Recreational fishing in the Great Lakes today exceeds commercial fishing in economic value and has the potential to influence fish stocks. Because it is difficult to quantify the spatial extent of recreational fishing by individuals, we focus solely on charter boat recreational fishing. We assume that this approximates the intensity and spatial distribution of all forms of recreational fishing (63), but we also acknowledge that private boats may travel lesser distances from shore. A list of all charter fishing boats operating on the Great Lakes was compiled from state and provincial regulatory agencies, such as Departments of Natural Resources and by searching the Internet. Latitude/longitude coordinates were obtained from marina locations or from Web sites and Google Earth. We identified 1,834 charter fishing services operating on the Great Lakes, with most located on Lakes Michigan (698) and Erie (814), and fewer on Lakes Ontario (143), Huron (78), and Superior (80). Salmon, steelhead, and lake trout were principal target species in all but Lake Erie and Lake Huron, where walleye (especially since 2000), yellow perch, and smallmouth bass were primary fish species listed on charter fishing Web sites. The spatial extent of charter fishing was estimated using the number of boats at each location as the magnitude of effect, and propagated into each lake assuming that only 10% of boats fish beyond 27.5 km from port and that the number was negligible beyond 55 km. Direct queries to a number of charter fishing operators in each lake indicate that travel distances <20 km are typical, although boats occasionally travel greater distances.

Aquaculture. Aquaculture is a growing industry in inland waters of the Great Lakes basin, but lake-based cage culture, which began in the mid-to-late 1980s (64), occurs only in Georgian Bay and North Channel of Lake Huron. Aquaculture can be detrimental to its immediate surrounding environment, affecting water quality via food byproducts and excreted waste from fish, leading to organic and nutrient enrichment and eutrophic conditions. Other potential problems include introduced diseases and parasites and antibiotic use. Because rainbow trout, although a nonnative species, are already established in the Great Lakes, the most likely impact of trout aquaculture is through degradation of water quality. Aquaculture locations were derived from Canadian Aquaculture Systems, Inc. and located visually using Google Earth to generate a point file of aquaculture pen locations. Ontario cage operations are reported to use low P, high digestibility feeds (65) and produce both particulate waste from fish feces and feed and dissolved nitrogenous wastes from gill and urinary excretions (66). The majority of solids may sediment within hundreds of meters of cage locations, whereas ammonium nitrogen levels have been reported to return to background at distances of 0.5–12 km. Water circulation patterns will substantially influence the extent of flushing as well. We assume that water quality effects are local, dissipating to 10% of their initial value within 5 km and to 1% within 10 km.

Native fish stocking. Across the Great Lakes, native fish stocking has been pursued for the rehabilitation of native fishes and restoration of native fish communities. Although it is unlikely to be an important stressor, any stocking activity has the potential to introduce disease organisms, alter the population's genetic makeup, and affect species interactions. Lake trout, lake sturgeon, Atlantic salmon, and walleye currently are stocked in some locations. Fish stocking data were derived from the Great Lakes Fish Stocking Database maintained by the Great Lakes Fishery Commission. Stocking data for native species were obtained for the years 1999–2008 for all lakes. These data, summarized by 10-min grid cell where they enter the Lakes, were then associated with a point at the center of the cell before propagating the data into the lakes. Dispersal was estimated based on several studies of fish movements. Lake trout dispersal is relatively limited, with the majority of recaptures of tagged fish occurring within 60–80 km of release. In contrast, stocked salmon appear to exhibit high mobility and seasonal migrations (67, 68). Because the majority of native fish stocked are lake trout, which disperse less than nonnative salmonids, we assumed that only 10% of stocked native fishes dispersed more than 50 km, and only 1% went as far as 100 km.

Nonnative fish stocking. Atlantic salmon, brown trout, Chinook salmon, coho salmon, and rainbow trout are all currently stocked in one or more of the Great Lakes (69). The stocking of nonnative salmonines may provide vectors for disease and parasite introductions and for disease and parasite spread throughout the Great Lakes because of to the mobility of stocked salmonines. Furthermore, nonnative salmonines may compete with native fishes for food and spawning habitat and may cause excessive mortality to native prey and competitor species (70). On the other hand, stocked nonnative salmonines are among the most effective controls of alewife and rainbow smelt abundances and have facilitated the recovery of native fishes in Lakes Huron (71) and Michigan (72). Nonnative salmonines also play a key role in the regional economy through support of profitable sport fisheries (68). Hence, nonnative salmonine stocking plays an ambiguous ecological role with the potential to both harm native species and to facilitate rehabilitation of diminished, threatened, or extirpated native species. Nonnative fish-stocking data were derived from the Great Lakes Fish Stocking Database for the years 1999–2008. Methods are identical to those of the native species. Because the majority of nonnative fish stocked are Chinook salmon, coho salmon, and rainbow trout, which disperse widely (67, 68), we assumed that 10% of stocked nonnative fishes dispersed 100 km and 1% traveled as far as 150 km.

Category: Invasive Species. As of 2012 over 180 nonindigenous species were reported in the Great Lakes (73), making this ecosystem arguably the most invaded freshwater system on the planet (74). However, many nonindigenous species cause little harm (75) and some may provide positive ecological benefits. We convened an expert workshop to identify nonindigenous species as well as native nuisance species that are important threats to the Great Lakes. Workshop participants expressed greatest concern for the influence of dreissenid mussels (zebra and quagga), the sea lamprey, round gobies, wetland plants (represented by *Phragmites*), sublittoral plants (represented by Eurasian milfoil), rusty crayfish, certain zooplankters (*Bythotrephes longimanus* and *Cercopagis pengoi*), harmful algal blooms, and emerging fish diseases (represented by viral hemorrhagic septicemia). Ballast water risk received some concern but may be declining in importance. We were able to acquire sufficient data to map five of these.

Zebra and quagga mussels. Zebra mussels (*Dreissena polymorpha*) first appeared in the Great Lakes in Lake St. Clair in 1986 (76), followed by quagga mussels (*Dreissena bugensis*) in 1989 (77). *Dreissena* colonization has resulted in a number of physical and chemical changes to the Great Lakes. Colonization adds habitat complexity for benthic invertebrates and creates a hard substrate in soft-sediment systems. Chemical impacts are complex and variable, as numerous studies have found dreissenid effects on total phosphorus (TP), soluble reactive phosphorus, nitrate, turbidity, and chlorophyll levels (78). When in high density, dreissenids appear to cause chlorophyll declines (79) and shunt pelagic algal production into benthic mussel biomass (80), possibly reducing food availability to upper trophic levels and thus limiting fish productivity. In addition, dreissenids may facilitate growth of the nuisance algae *Microcystis aeruginosa* (81) and *Cladophora glomerata* (82) because of increased water clarity (78), although the public may perceive greater underwater visibility as a benefit (83). Data on *Dreissena* distributions in numbers per square meter at point locations were acquired from research scientists throughout the Great Lakes region. To obtain estimates of density over the Lakes as a continuous surface, the combined densities of zebra and quagga mussels were kriged by lake.

Sea lamprey. Sea lamprey (*Petromyzon marinus*) invaded Lake Ontario in the early 19th century and expanded throughout the Great Lakes in the mid-20th century. The sea lamprey is considered one of the most detrimental invasive species to enter the Great Lakes (84), and is known to parasitize lake trout, nonnative salmonines, lake whitefish, lake herring, rainbow trout, burbot, and walleye. Although the sea lamprey was not solely responsible for all population collapse of lake trout, it is currently a major impediment to lake trout rehabilitation efforts (85). The abundance and distribution of sea lampreys throughout the Great Lakes has not been determined. However, adults enter rivers to spawn, and spawning numbers are estimated from surveys and modeling (86). Estimates of the number of spawning adults per river during 2000–2009 were acquired from the Great Lakes Fishery Commission and used as a proxy for the distribution and relative abundance of young lampreys seeking hosts. There is limited information on the distance traveled by host-seeking lampreys and the additional dispersal distance that occurs by "hitch-hiking," but distances likely are comparable to salmonine dispersal estimates given above. A mark-recapture study from northern Lake Huron reported that 78% of recaptures were within 100 km of release (87); in Lake Champlain lampreys were captured up to 64 km from natal streams (88). We estimated the lake area most affected by parasitic sea lampreys using an exponential decay model with the assumption that only 10% traveled as far as 100 km from their natal river, and only 1% dispersed as far as 150 km.

Ballast water invasion risk. Since the opening of the St. Lawrence Seaway in 1959, ballast water release from ocean vessels is the most probable vector for almost two-thirds of invasions, including some of the most notorious Great Lakes invaders such as zebra and quagga mussels and round gobies (74, 77). Because of the importance of ballast water release as an invasion pathway, control measures have been enacted. Ballast water exchange, the exchange of fresh or estuarine water with sea water to purge or kill organisms in ballast tanks, has been required since 1993. Saltwater flushing instituted after 2006 further requires sea water rinsing of ballast tanks of Great Lake-bound ships. The effectiveness of these control measures remains a matter of debate (89, 90), although the importance of ballast water as a pathway likely is diminishing (91). However, ballast discharges from ships confined to the Great Lakes account for 95% of all ballast water discharges and may facilitate the secondary transport of species that have already been introduced (92). As a proxy for propagule pressure, we mapped the total volume of ballast water discharged at each port using discharge data from a recent ballast water risk assessment carried out by the Canadian Department of Fisheries and Oceans (18). Correction factors of 0.1 and 0.01 were applied to discharge volumes from foreign and coastal vessels, respectively, to account for the reduction in propagules that occurred as a result of ballast water management activities such as ballast water exchange or saltwater flushing. Propagule pressure is only one factor affecting invasion success (93), which also is facilitated by favorable environmental conditions and release into sheltered areas to limit physical dispersion (94). Tracer particles released into the semienclosed port of Goderich, ON, Canada, showed rapid dilution, with some particles were collected up to 7.5 km outside the harbor (94). We assume that propagules of invasive species introduced from ballast water are concentrated in the vicinity of the port and decay to 10% of their initial abundance in 2.5 km and to 1% at 5 km.

Round gobies. The round goby (*Neogobius melanostomus*) is a bottom-dwelling fish whose native range is in Eurasia. The round goby was first observed in the St. Clair River (95), presumably a ballast water introduction, and is now widespread in all Great Lakes except Lake Superior, where it is reported from only a few locations. It is especially abundant in Lakes Erie and Ontario. The round goby population of western Lake Erie was estimated at 9.9 billion individuals (96). The round goby preys on eggs and fry of other fish as well as benthic invertebrates. They frequent shallow waters (<15–20 m) during the warm season and some migrate to deeper waters (80 m or more) during winter. The impact of round gobies on lake ecosystems is variable. Declines in native species have been ascribed to both predation and competition (97, 98). Round gobies have also been implicated in the spread of botulism to piscivorous birds (99). On the other hand, gobies heavily consume zebra mussels and are themselves consumed by piscivorous sports fish, such as smallmouth bass (100). We obtained records of observed round goby locations within the Great Lakes and from rivers within 5 km of the Lakes. We modeled habitat suitability for round gobies based on environmental variables hypothesized to influence goby distributions: average summer temperature (over the warmest 3 mo for 17 y, July 1–September 30, 1994–2010), average chlorophyll a levels in May 2008 (based on SeaWiFS satellite imagery), depth, and dreissenid densities. We ran models both with and without substrate type, but the resulting models were statistically equivalent, so we present results from the model without substrate. Models were run in Maxent software with default settings, and they were validated with 10-fold cross-validation and test omission. The resulting model was highly discriminative based on standard performance measures (mean area under the curve = 0.94). The predicted habitable locations for round gobies represent probable extent of occupancy and do not reflect relative abundance. This map also excludes deep-water observations, which are too few to model at present and generally are from autumn and winter surveys.

Wetland plants: Phragmites. Invasive common reed *Phragmites australis* subspecies *australis* forms dense monocultures, which crowd out native plants, inhibit animal movement, serve as a poor quality food for animals, and slow decomposition (101). In freshwater habitats, evidence suggests decreases in turtle, bird, and amphibian populations, plant diversity, nutrient cycling, and microhabitat conditions (102–104). Although several genotypes of *P. australis* (subspecies *americanus*) are native to North America, exotic genotypes (particularly haplotype M from Europe) have been present in the Great Lakes region since the 1910s and expanded rapidly starting in the 1960s, nearly entirely displacing the native genotypes (102, 105). Invasive *Phragmites australis* location data came from three sources: (*i*) United States only: estimated occurrences of large monotypic stands on land 0–10 km from the Great Lakes shoreline derived from PALSAR remote sensing imagery (106); (*ii*) Canada only: georeferenced point occurrences from Ontario Natural Heritage Information Centre (107); and (*iii*) Canada only: georeferenced point occurrences from Global Biodiversity Information Facility (108). Both subspecies *australis* and unknown subspecies records were used from the Canadian datasets, but unknown subspecies records in Lake Superior were eliminated because they were likely the native subspecies [no subsp. *americanus* found in extensive surveys along Lake Superior (106)]. We used a 10-km shoreline buffer to eliminate observations further inland. Roadside Canadian locations were converted to stands using a 500-m buffer on the assumption that these were stands too small to be detected in the remote sensing data. For all other Canadian observations, we used a 5-km buffer, because *Phragmites* dispersal distances are frequently this large (109). To propagate the effects of the stands (most of which were on land) into the lakes, for every 1-km^2 waterside shoreline pixel, we calculated the distance to the nearest invasive *Phragmites* patch. We normalized these data assuming that closer proximity to *Phragmites* had stronger negative effects (intensity 0 = no effect of *Phragmites* because all stands were >10 km away; intensity 1 = *Phragmites* stand located in that pixel).

Category: Nonpoint Pollution. Run-off from land includes materials transported by surface and subsurface (including through infrastructure) run-off. We consider materials that originate from both point and diffuse sources, including watersheds and atmospheric sources. We use four data layers: inputs of suspended sediments, nitrogen, phosphorus, and combined sewer overflows (CSOs) to the Great Lakes.

Suspended sediments. Sediments exported from rivers cause turbidity, which can interfere with algal growth and prey location by visual predators, and alter benthic habitat conditions. Annual loads of suspended sediments (SS) were obtained from several sources (110–113). Data for Canadian tributaries were averages for 1972–2005, except tributaries for Lake Superior, which were averages for 1990–2009. Data for US tributaries were averages for 1975–1990, and some Lake Erie tributary data were averages for 1997–2001. Because locations with SS data only partly aligned with our list of major tributaries with nitrate and TP data, we estimated missing SS loads using lake-specific regressions of sediment load against watershed area, and examined all estimated values for consistency with neighboring sites. Forty of the 119 sites were regression estimates (Lake Superior, 6; Lake Michigan, 12; Lake Huron, 9; Lake Erie, 10; Lake Ontario, 3).

Annual sediment loads were propagated from river mouths using an exponential decay model as described above (*SI Materials and Methods*). Because most of the load is delivered during episodes of high run-off, which tend to occur in the winter and spring, we examined satellite images of river plumes during high run-off events to estimate dispersal of transported material. Mapping of the Maumee River plume using MODIS imagery adjusted with observed Secchi disk transparency (113) found plume extent to vary among dates and years. Plumes are deflected along the southern shore of Lake Erie by inflow from the Detroit River, with typical extent of ~10 km outward and 25 km along the southern shore. We infer that a decay coefficient that reduces the sediment load to 10% of its initial value over a distance of 10 km is reasonable. Plumes were terminated at 1% of initial value, which occurred in ~20 km. We acknowledge that sediment transport may differ among locations due to along-shore currents, natural embayments and man-made harbor structures.

Nitrogen. Various forms of nitrogen in fresh water may stimulate algal growth and contribute to eutrophic conditions. Nitrogen input to the Great Lakes is represented by nitrate (+ nitrite), which typically comprises the majority of total inorganic nitrogen. Tributary nitrate loads were averaged for 1994–2008 except for Lake Erie, where tributary data were available only for 2005 (114). However, whole lake totals for Lake Erie were available for 2003–2007, and establish that 2005 was a midrange year. These estimated inputs include the most important tributary sources and comprise ~60–80% the total tributary load to each lake, because of the omission of small watersheds the inclusion of which is impractical. Atmospheric deposition of nitrate to the lakes' surfaces was estimated using National Atmospheric Deposition Program data for wet nitrate deposition and Clean Air Status and Trends Network (CASTNET) data for dry deposition. To provide a 5-y average of total atmospheric deposition of nitrate, 2003–2007 CASTNET (dry deposition) data were downloaded for all neighbor sites of the Great Lakes Basin, and 5-y averages of dry-to-wet deposition ratios were calculated. To obtain a data layer for total deposition of nitrate-N (dry + wet), wet deposition was multiplied by (1 + dry to wet ratio) using ArcGIS, following methods in Han and Allan (115). Estimated tributary and atmospheric inputs are consistent with other estimates for the Great Lakes region (115–117). Tributary loads were propagated spatially based on the assumption that because nitrate is exported as a solute it decays more slowly than sediments, declining to 10% of initial levels at 15 km and 1% of initial at 30 km. Propagated nitrate was then combined with atmospheric deposition over the lake surface.

Phosphorus. Phosphorus run-off from watersheds is considered the most important driver of eutrophication and the proliferation of nuisance algae. Phosphorus inputs to the Great Lakes are represented by TP, and include both tributary and atmospheric inputs. Tributary TP loads from Dolan and Chapra (114) were averaged for 1994–2008 except for Lake Erie, where tributary data were averaged for 2003–2007. Because the watersheds of included tributaries encompass only 60–90% of the total drainage area of each lake, estimated tributary loading of TP is likewise reduced. Atmospheric deposition of phosphorus to the surface of the Great Lakes is a small amount and not well quantified, with estimates ranging from 5 to 25 $kg \cdot km^{-2}$ (118). We used an average value of 8 $kg \cdot km^{-2}$ across the upper lakes and 16 $kg \cdot km^{-2}$ for Lake Erie and Lake Ontario. Tributary phosphorus loads include particulate P associated with fine sediments and dissolved P; because dissolved P is considered more biologically available and P associated with fine particles may dissociate into soluble form in response to concentration gradients, we elected to use the same decay coefficient as for nitrogen. Tributary loads were propagated spatially based on the assumption that loads declined to 10% of initial levels at 15 km and 1% of initial at 30 km. Propagated TP was then combined with atmospheric deposition over the lake surface. The resultant spatial patterns are broadly consistent with published TP contours for Lake Erie (119) and Lake Ontario (120).

Combined sewer overflows. Combined sewers that collect sanitary sewage and stormwater run-off into a single pipe system are found in many Great Lakes cities, where overflows can occur during heavy storms. Under wet weather conditions, high stormwater volumes may result in the discharge of untreated sewer waste into surface waters. In addition, stormwater may contribute pollutants, such as oil and grease from vehicles, fecal bacteria from pet and wildlife waste, and pesticides and lawn chemicals that accumulate on diffuse surfaces during dry periods. We obtained the number of CSO outfalls for US communities within 10 km of the Great Lakes shoreline from the US EPA (121). We used a combination of state agency reports to determine CSO discharge volumes. When discharge volume data were not available, we estimated discharge based on the number of outfalls present using a log-linear regression between discharge volume and number of outfalls (Adjusted R^2 = 0.59). Although Chicago's 369 CSO outfalls normally discharge away from Lake Michigan, heavy and sustained rainfall can cause 303 of Chicago's outfalls to empty into the lake. Information on CSO contributions from communities and estimated discharge volumes for Canadian cities was obtained from MacDonald and Podolsky (122). Although our data contain a number of uncertainties, we were able to estimate CSO discharge volume for 48 cities bordering the Great Lakes in millions of gallons per day. Surveys of the near shore of western Lake Ontario found that levels of solids, major ions, and *Escherichia coli* declined sharply away from shoreside areas, with little or subtle decline beyond 1–3 km (123). We assumed that the influence of CSO discharge declined to 10% at 3.5 km from an outfall and was negligible beyond 7 km.

Category: Toxic Chemicals. The Great Lakes are influenced by a great diversity of toxic chemicals, including legacy and current contaminants, as well as chemicals of emerging concern. We characterized toxic chemicals with data layers for mercury, copper, and polychlorinated biphenyl compounds (PCBs). Because the majority of the areas of concern (AOCs) in the Great Lakes are associated with contaminants we included the 39 remaining AOCs as a fourth stressor.

Mercury. Mercury is an important toxic substance affecting human and ecosystem health in the Great Lakes (124, 125), and an example of a biomagnifying toxic metal. Human exposure to methylmercury in the Great Lakes basin is primarily through freshwater fish consumption (126). We mapped surficial sediment mercury concentration using near-shore values obtained from a collection of monitoring projects compiled by the NOAA Assessment and Restoration division and in-lake values collected by the sediment monitoring program by Environment Canada (127). Data were kriged using ArcGIS algorithms with a five-point neighborhood.

Copper. Metal contamination including lead, nickel, copper, zinc, and cadmium may harm organisms at low concentrations if the metal compounds are in a bioavailable form, but rarely cause ecological effects through biomagnification. We focus on copper as an industrial metal of concern known to occur at elevated concentrations in the Great Lakes. Copper can be highly toxic at low concentrations to invertebrates and to fish in early life stages (128) and can result in food web disruption. We mapped surficial sediment copper concentration from two data sources. Near-shore datapoints were obtained from collection of monitoring and restoration projects (as for mercury), and in-lake data values were provided by Environment Canada (129). Data were kriged using ArcGIS algorithms with a five-point neighborhood.

PCBs. PCBs are a class of legacy organochlorines that share a structural similarity and toxic mode of action with Mirex, Toxaphene, and dioxin, all known to exert multiple toxic effects throughout the food web in lakes (130). PCBs were widely used as coolants and insulating fluids and in a variety of other industrial uses, but their manufacture and importation to North American ended in 1977–1980. As with other restricted legacy organochlorines, PCBs are extremely resistant to degradation and persist for decades in the environment. Like methylmercury, PCBs bioaccumulate rapidly through food chains, resulting in restrictions on fish consumption (131) and concerns for wildlife health (130). We mapped surficial sediment PCB concentrations from Environment Canada (129). Data were kriged using ArcGIS algorithms with a five-point neighborhood.

Areas of Concern. The US EPA and Environment Canada designated 43 AOCs under the Great Lakes Water Quality Agreement, a binational agreement to ensure the long-term maintenance of the "chemical, physical, and biological integrity of the Great Lakes Ecosystem" (132). Sediment contamination is the most common cause of AOC listing. AOCs range in size from those covering entire watersheds to portions of watersheds, segments of rivers, stretches of shoreline, and individual bays and harbors. Generally, the AOCs are associated with a river mouth, and their area of influence in the lakes themselves is largely undefined. However, sediment contamination is generally localized at river mouths and harbor areas of human dominated watersheds, where fine-grained sediments have been deposited over time (133). We represent the influence of the 39 remaining AOCs (four have been delisted) on the Great Lakes by first eliminating those located more than 10-km inland from the shoreline. For 13 AOCs, where the official AOC boundary extended into a Great Lake, we used that boundary to define the area of influence. The influence of remaining AOCs was spatially delineated as an area extending 5 km from the river mouth. All AOCs were considered to exert equal stress.

SI Ecosystem Services

We use the locations of beaches, marinas, and important bird-watching sites to represent high-value recreational activities. To address provisioning services, we quantify two aspects of fisheries: the spatial distribution and magnitude of commercial harvests, and the home port for charter fishing vessels. We also assess spawning locations for two important species in recreational and commercial fisheries: lake trout and yellow perch. We investigate the spatial correspondence between each service and CS by testing whether the rank order of locations for a given service (e.g., each beach) is random with respect to CS values of all pixels. The 1:1 line reflects the null hypothesis that locations of service provisioning are randomly distributed across all stress levels (Fig. 4*C*). Although it was not feasible to assign a use or value to each service at each location, all seven measures warrant inclusion as ecosystem services. Commercial fishing, recreational fishing by charter boat, and recreational boating from marinas each could in principle be quantified directly, whereas human visitation of birding and beach sites, and use of spawning sites by lake trout and yellow perch, are more difficult. Birding locations were selected by expert consultation (see below) and represent a modest number of highly valued sites from a much larger potential pool. It is not feasible to demonstrate that every beach and spawning site is used, but it is a reasonable assumption that all deliver some service over multiple years.

To explore the assumption that CS is the appropriate measure of stress, we identified a subset of 3–10 stressors likely to have the greatest impact on each specific service (Table S3), and recalculated a new stress index specific to each service. The disproportionately high stress at service locations remained evident in this refined analysis (Fig. 4*D*), although the skew was slightly less pronounced for most services. This service-specific analysis supports the conclusion that sites where society depends upon ecosystem services from the Great Lakes are generally more stressed than expected by chance.

We estimated stress (CS or service-specific) for each service with a 5-km buffer around the service point. Although it is likely that some services (e.g., beaches) are sensitive to stress at a smaller scale, we chose to use 5-km buffers in all instances for consistency and to reduce the risk that an individual pixel might be an outlier.

Beach Use. The annual recreational value of Ontario's Great Lakes beaches has been estimated at C$200–259 million (134), and the US Great Lakes beaches have been valued at US$1.1–1.4 billion (135). As with the stressor layer, American beach locations were derived from the US EPA BEACH Act Geospatial database. US beaches were represented by line segments, which we converted to points using the midpoint of each segment. The locations of Canadian beaches were provided by Environment Canada, and a small number of additional beaches were identified from protected lands databases for the United States and Canada (Fig. S5*A*). We created a stress metric specific to beaches summing five individual stressors considered most likely to adversely affect beach use (Table S3).

Recreational Boating. Recreational boating and boating-related expenditures in the US Great Lakes totaled an estimated $16 billion and directly supported 107,000 jobs in 2003 (34). We used the locations of marinas (Fig. S5*B*) to represent the spatial distribution of recreational boating on the Great Lakes from the data layer reported earlier. We created a stress metric specific to recreational boating by summing four individual stressors considered most likely to adversely affect this activity (Table S3).

Birding. The Great Lakes basin is home to an estimated 5 million birding enthusiasts who frequent shoreline hotspots during all seasons (60). Across the United States, an estimated 48 million US residents engaged in bird-watching activities, adding $82 billion to the US economy in 2006 (136). We mapped locations representing the most highly used and valued birding hotspots in the Great Lakes region that were located within 2 km of the shoreline using data from several sources, including recommendations of top birding locations from state and provincial bird record committees and ornithological organizations, recognized "birding hotspots," sites along birding trails, and sites hosting birding festivals. Our mapped birding locations represent areas adjacent to the Great Lakes where birding activity is most concentrated (Fig. S5*C*). We created a stress metric specific to birding by summing three individual stressors considered most likely to adversely affect this activity (Table S3).

Recreational Fishing. Between the United States and Canada, an estimated 1.8 million anglers report fishing on the Great Lakes (137, 138). Because fishing by individuals is difficult to quantify, we used charter fishing as a measure of recreational fishing effort. In Michigan alone, charter fishing contributed nearly $15 million in gross sales to coastal communities (139). Fig. S5*D* shows the spatial distribution of charter fishing. We created a stress metric specific to recreational fishing by summing ten individual stressors considered most likely to adversely affect this activity (Table S3).

Commercial Fishing. The spatial distribution of commercial fishing (Fig. S5*E*) exhibits only partial overlap with charter fishing, because the former targets primarily lake trout, lake whitefish and chubs, and the latter primarily nonnative Pacific salmonids, walleye, and yellow perch. Spatial overlap between commercial and recreational harvest of lake trout and lake whitefish is further reduced by harvest treaties negotiated with Native American tribes and establishment of lake trout refuges. However, there is overlap, particularly over harvest of yellow perch and walleye in Lake Erie and Saginaw Bay of Lake Huron, and nontribal harvest of lake trout in the upper lakes. We created a stress metric specific to commercial fishing by summing ten individual stressors considered most likely to adversely affect this activity (Table S3).

Lake Trout Spawning. Lake trout are valued by recreational and commercial fishers. In addition, as a native species in decline they are stocked in several lakes to encourage recovery. Thus, spawning areas are important to natural recruitment. Lake trout spawning locations were derived from the *Atlas of Spawning and Nursery Areas of Great Lakes Fishes*, a comprehensive binational survey of commercially and recreationally valuable fishes (140). Records of lake trout spawning occur primarily in Lakes Superior, Michigan and Huron. Lake trout are fall spawners that require cold water (3–14 °C) and rocky substrate with adequate interstitial spaces to protect eggs from predators and wave action (140, 141). Fig. S5*F* shows the spatial distribution of lake trout spawning locations, which we assume are all used. We created a stress metric specific to lake trout spawning by summing seven individual stressors considered most likely to adversely affect this activity (Table S3).

Yellow Perch Spawning. Yellow perch also are valued by recreational and commercial fishers, and their spawning areas are important to natural recruitment. Yellow perch spawning locations were again derived from the atlas developed by Goodyear et al. (140). Wei et al. (142) found the distribution of yellow perch to be highly correlated with coastal wetlands, and suggested that yellow perch favor protected embayments in particular for spawning and nursery habitat. Fig. S5*G* shows the spatial distribution of yellow perch spawning locations, which we assume are all used. We created a stress metric specific to yellow perch spawning by summing nine individual stressors considered most likely to adversely affect this activity (Table S3).

SI Multivariate Analyses of Areas of High Stress

If a small number of stressor intensity combinations caused high CS values, we expected nonhierarchical cluster analysis would allow us to identify this pattern. We used the *K*-means algorithm in R (143) with 1–20 clusters (10 random starts, maximum 25 iterations, other settings default). The amount of variation explained by each additional cluster decreased steadily without an obvious breakpoint, suggesting no small number of clusters that captured the variation among pixels well (Fig S6*A*). Inspection of resulting clusters (e.g., six-cluster solution in Fig. S6*B*) indicated that many different combinations of stressor intensities were responsible for the high CS scores.

We also performed principal components analysis (PCA) using the prcomp() algorithm in R (143) to assess whether linear combinations of stressor intensities could summarize most of the variation among high stress pixels. Assumptions of PCA, such as multivariate normality, were not fully met, but this technique is still acceptable for exploratory purposes under these circumstances (144). No rescaling was used in the computations, because the data were already transformed to similar scales. For plotting only, we rescaled loadings (arrows in biplot, Fig. 3*C*) based on the minima and maxima of site scores and factor loadings. We found the first two components to account for 32.7% of the variation in stressor intensities (axis 3 = 9.2%, axis 4 = 7.6%). Many of the same stressors that had high correlations with the overall CS map (Fig. 3*A*) loaded highly on the first two PCA components (Fig. 3*C*), and the first two components captured gross differences among the high stress areas across lakes (Fig. 3*C*). However, as expected from cluster analysis results, the resulting biplot showed no major clustering of sites (Fig. 3*C*). This result again suggested that no discrete sets of stressors are predictably high in a given high stress area.

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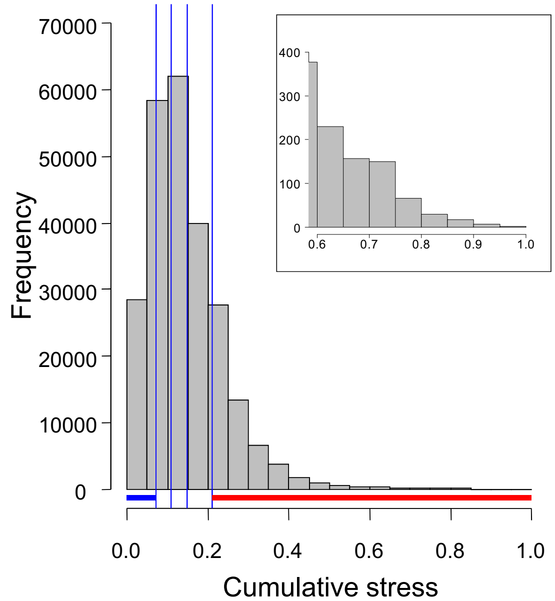

Fig. S1. Histogram of CS in the Laurentian Great Lakes. Frequencies are the area (in square kilometers) in each bin (n = 243,937 pixels). (*Inset*) Expanded view of tail values. Quintile breaks in CS (drawn with vertical lines) are: 0% = 0, 20% = 0.07, 40% = 0.11, 60% = 0.15, 80% = 0.21, 100% = 1. We highlight the lowest quintile in dark blue and the highest quintile in red, which correspond to the dark blue and red regions in Fig. 1.

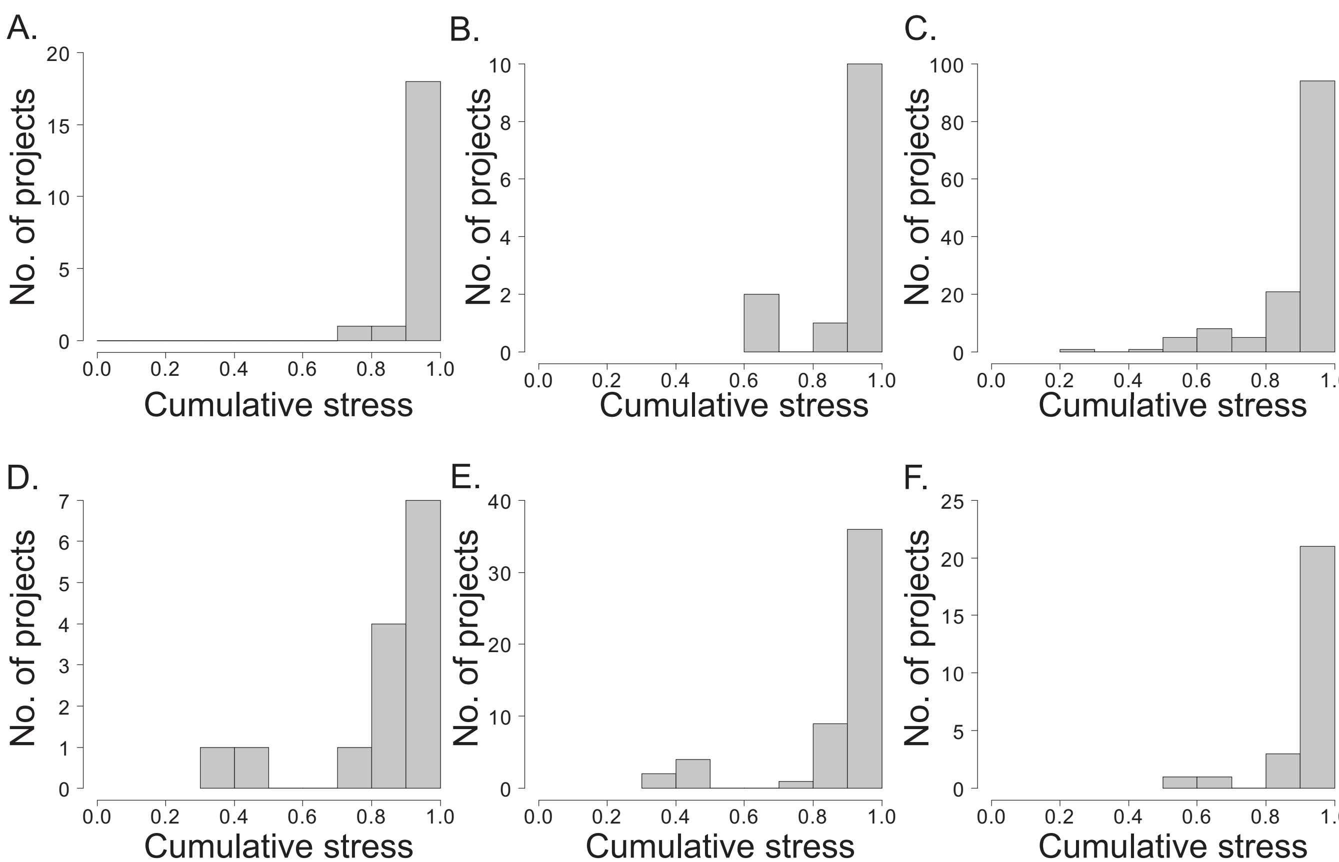

Fig. S2. Current restoration activities in the Laurentian Great Lakes are located primarily in areas of high CS. Histograms of CS at AOCs, separated by location type (*A* and *B*), and restoration projects funded through the US Great Lakes Restoration Initiative (GLRI), separated by focus area (*C*–*F*). (*A*) AOCs located in river mouths and connecting channels (n = 20); (*B*) AOCs located directly in the lake waters (n = 13); (*C*) GLRI projects focused on restoring wetlands and other habitats (n = 135); (*D*) GLRI projects focused on combating invasive species (n = 14); (*E*) GLRI projects focused on promoting nearshore health (n = 52); and (*F*) GLRI projects focused on cleaning up toxics (n = 26).

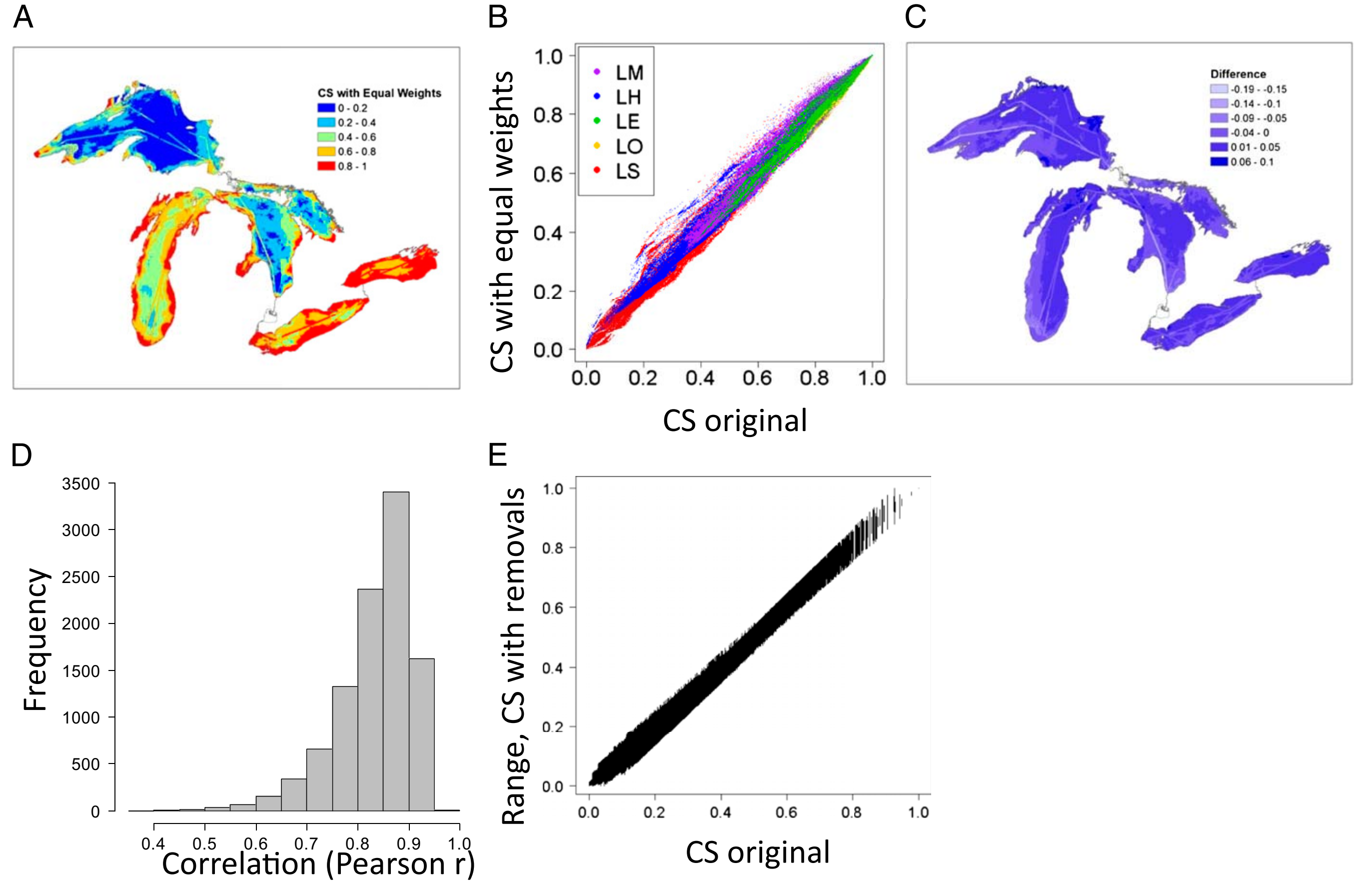

Fig. S3. Sensitivity analyses. (*A*) CS recalculated with the null expectation of equal weightings for every stressor (shown with ln[x + 1]-CDF transformation). (*B*) Plot of CS calculated with equal weightings vs. CS calculated with expert weightings mapped in Fig. 1, with each point representing one pixel in the Great Lakes (n = 243,937 pixels). Points are colored by lake (LM, Lake Michigan; LH, Lake Huron; LE, Lake Erie; LO, Lake Ontario; LS, Lake Superior). (*C*) Difference between CS using equal weightings and the original CS calculated with expert weightings. (*D*) Histogram of Pearson correlation coefficients from 10,000 permutations of the weightings; for each permutation, we randomly assigned the weights for each stressor (mixing up the expert weights), recalculated the CS map, and then calculated its correlation with the original CS map. (*E*) Results after removing individual stressors and recalculating CS: each vertical line represents one pixel in the Great Lakes (n = 243,937 pixels), showing the range (line segments drawn between maximum and minimum) of values computed when removing each of the 34 stressors one at a time.

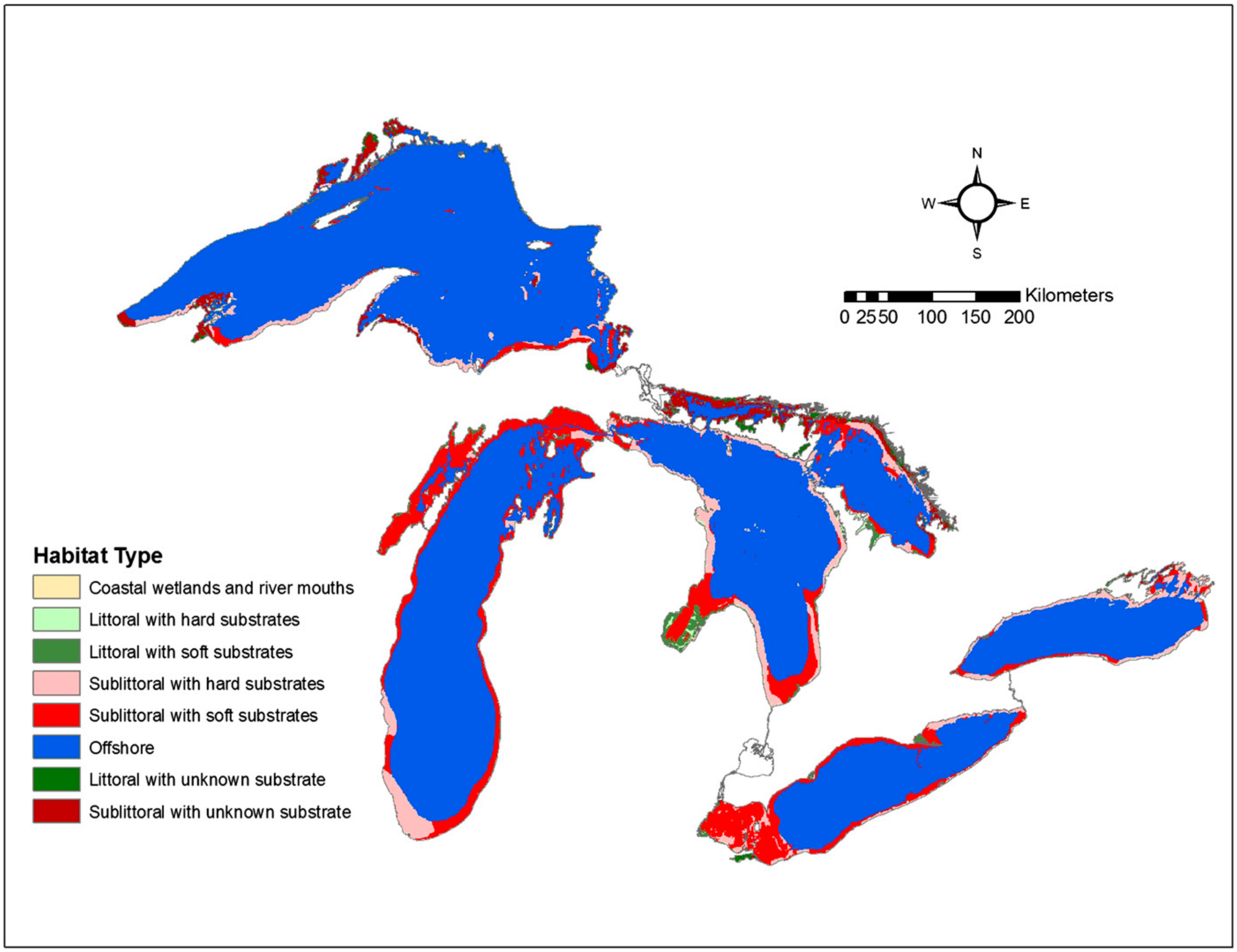

Fig. S4. The habitat classification for the Laurentian Great Lakes used for modeling cumulative stress.

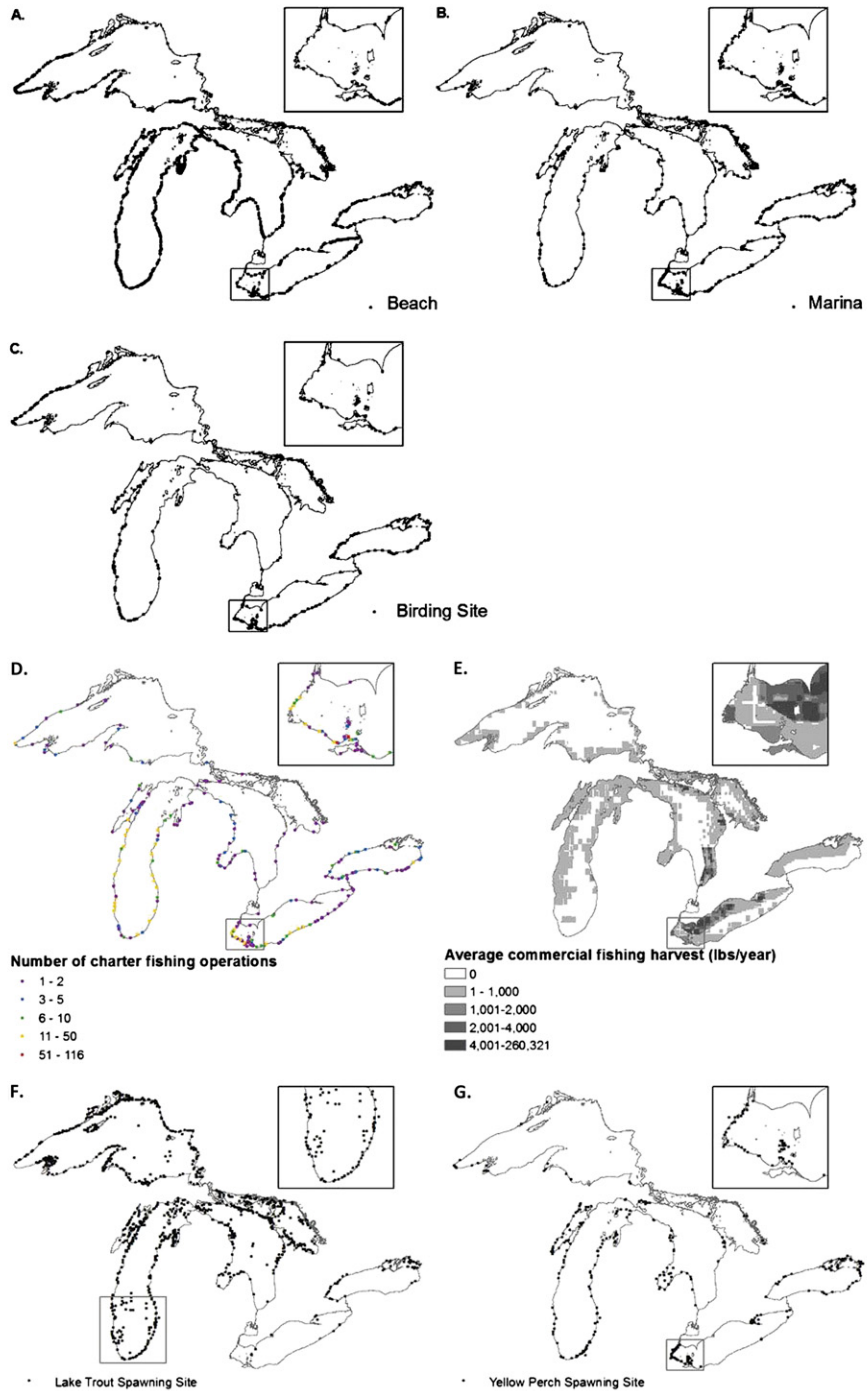

Fig. S5. Locations of ecosystem services. Some highly valued locations for recreational activities in the Laurentian Great Lakes include (*A*) beach locations, (*B*) marina locations, and (*C*) birding sites. Fisheries-related ecosystem services include two food provisioning services, charter and commercial fishing (*D*–*E*), and the locations supporting the spawning of two fish species caught in the Laurentian Great Lakes (*F* and *G*). Shown are (*D*) home ports of charter fishing operations, with colors depicting the number of boats operating out of each home port; (*E*) locations of commercial fishing harvest; (*F*) historic and current lake trout spawning locations; (*G*) historic and current yellow perch spawning locations.

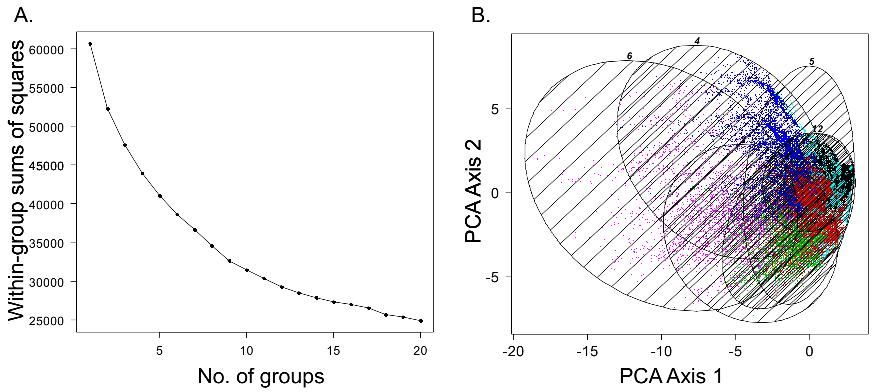

Fig. S6. Results from *K*-means cluster analysis of stressor intensities in high stress (CS > 0.8) areas of the Laurentian Great Lakes. (*A*) Modified scree plot showing the decrease in the within-group sums of squares with each addition of another cluster. (*B*) Example six-cluster result, summarized using PCA (29.7% of variation in stressor intensities explained): ellipses (numbered) represent each cluster in PCA space, and the sites (points) are colored by cluster. Note that PCA settings here are defaults from clusplot() in R, and they differ from the PCA biplot presented in Fig. 3*C*.

Other Supporting Information Files

Table S1 (DOC)
Table S2 (DOCX)
Table S3 (DOCX)