Joint analysis of stressors and ecosystem services to enhance restoration effectiveness

J. David Allan[a,1,2], Peter B. McIntyre[b,1], Sigrid D. P. Smith[a,1], Benjamin S. Halpern[c], Gregory L. Boyer[d], Andy Buchsbaum[e], G. A. Burton, Jr.[a,f], Linda M. Campbell[g], W. Lindsay Chadderton[h], Jan J. H. Ciborowski[i], Patrick J. Doran[j], Tim Eder[k], Dana M. Infante[l], Lucinda B. Johnson[m], Christine A. Joseph[a], Adrienne L. Marino[a], Alexander Prusevich[n], Jennifer G. Read[o], Joan B. Rose[l], Edward S. Rutherford[p], Scott P. Sowa[j], and Alan D. Steinman[q]

[a]School of Natural Resources and Environment and [f]Cooperative Institute of Limnology and Ecosystems Research, University of Michigan, Ann Arbor, MI 48109; [b]Center for Limnology, University of Wisconsin, Madison, WI 53706; [c]National Center for Ecological Analysis and Synthesis, and Center for Marine Assessment and Planning, University of California, Santa Barbara, CA 93101; [d]Great Lakes Research Consortium and College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210; [e]Great Lakes Regional Center, National Wildlife Federation, Ann Arbor, MI 48104; [g]Environmental Science, St. Mary's University, Halifax, NS, Canada B3H 3C3; [h]The Nature Conservancy Great Lakes Project, care of the Notre Dame Environmental Change Initiative, South Bend, IN 46617; [i]Department of Biological Sciences, University of Windsor, Windsor, ON, Canada N9B 3P4; [j]The Nature Conservancy Great Lakes Project, Lansing, MI 48906; [k]Great Lakes Commission, Ann Arbor, MI 48104; [l]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824; [m]Natural Resources Research Institute, University of Minnesota, Duluth, MN 55811; [n]Earth Systems Research Center, University of New Hampshire, Durham, NH 03824; [o]Michigan Sea Grant and Great Lakes Observing System, Ann Arbor, MI 48104; [p]Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, MI 48108; and [q]Annis Water Resources Institute, Grand Valley State University, Muskegon, MI 49441

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

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.

[1]J.D.A., P.B.M., and S.D.P.S. contributed equally to this work.

[2]To whom correspondence should be addressed. E-mail: dallan@umich.edu.

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

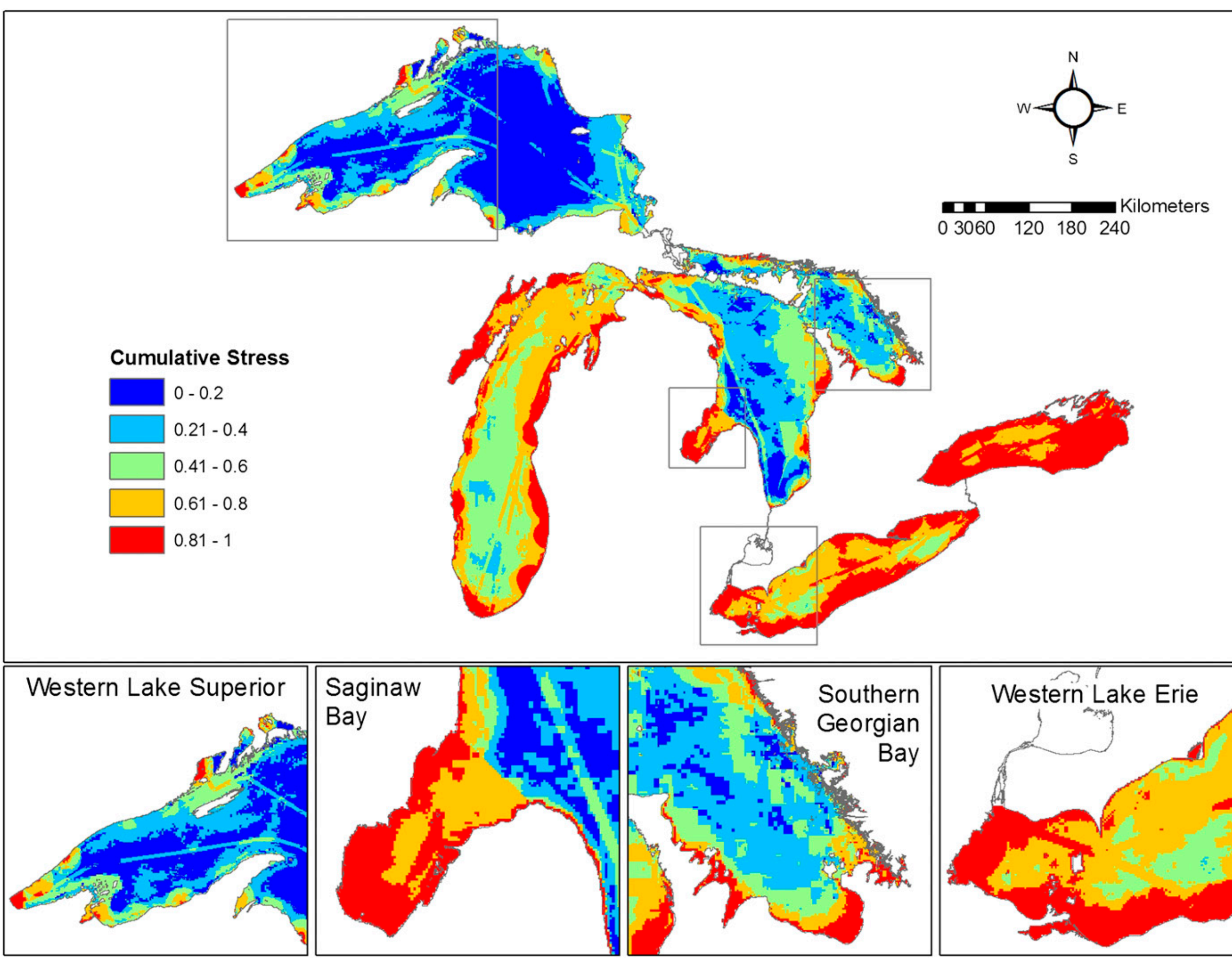

Fig. 1. The spatial pattern of CS from 34 human-induced stressors across the Laurentian Great Lakes and in selected regions. Cumulative stress was calculated based on the intensities of each stressor weighted by their impact (determined from expert judgment). We show CS on a relative (percentile) scale, 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.

SUSTAINABILITY SCIENCE

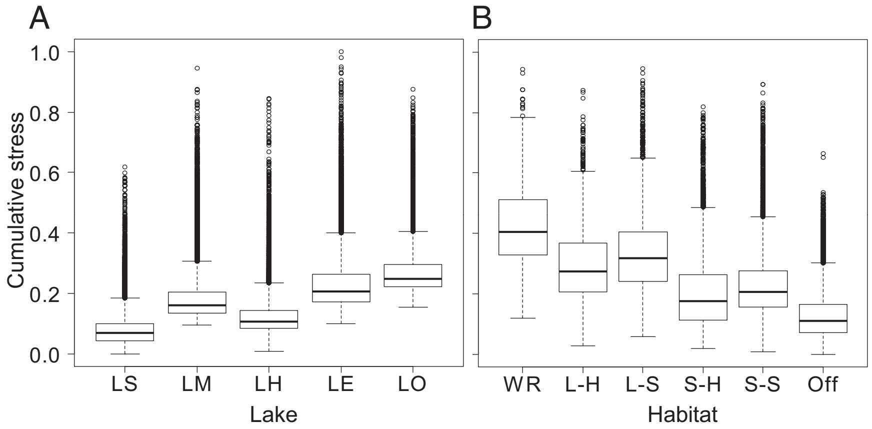

Fig. 2. Boxplots of cumulative stress for each lake (*A*) and habitat (*B*) in the Laurentian Great Lakes, showing medians and quartiles as boxes, 1.5× interquartile range as whiskers, and outliers as circles. Abbreviations used: Lakes Superior (LS), Michigan (LM), Huron (LH), Erie (LE), Ontario (LO); 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

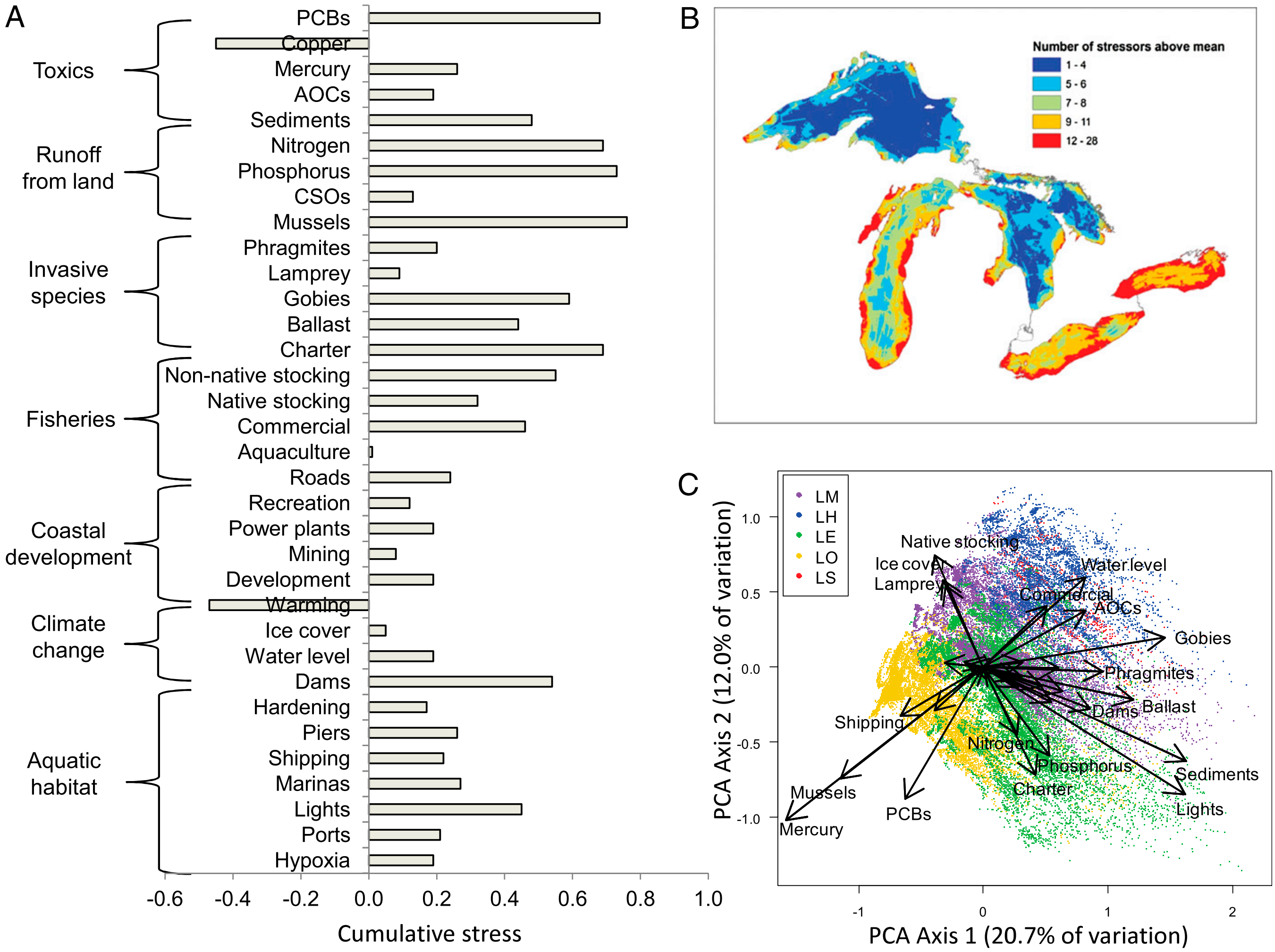

Fig. 3. Relationship between CS and individual stressor intensities in the Laurentian Great Lakes. (*A*) The correlation coefficient for each individual stressor map with the CS map, plotted as bars for better visualization. Because most stressors are positively correlated with CS (*A*), the number of 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),

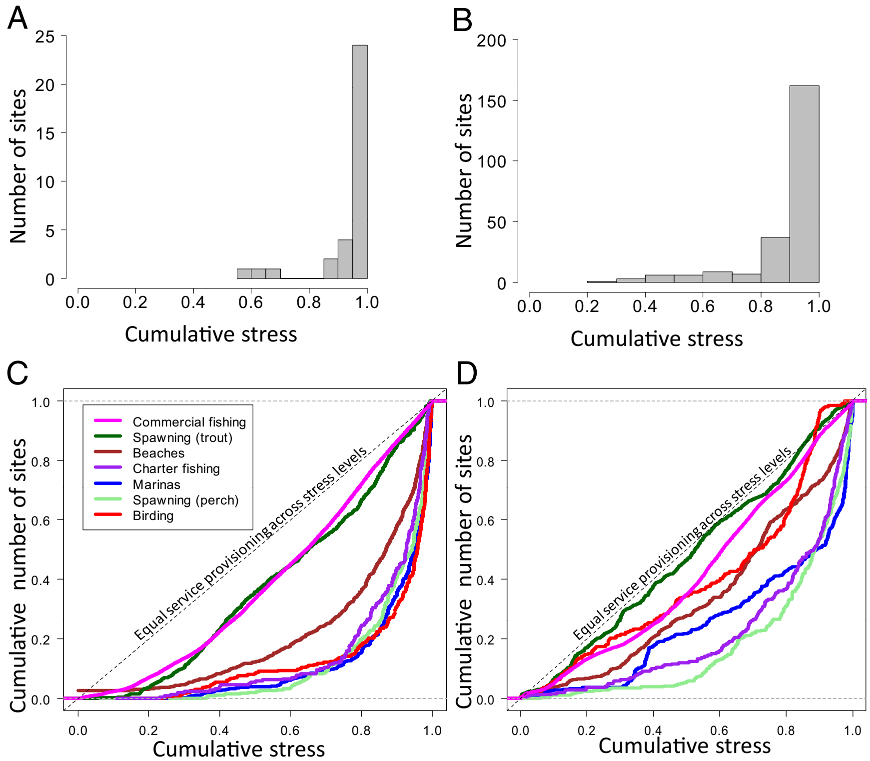

Fig. 4. Locations of current restoration efforts and valued ecosystem services coincide with areas of high CS in the Laurentian Great Lakes. Histograms of the frequency of CS at 33 AOC (*A*) and 231 GLRI sites (*B*) show that these sites are predominantly in locations with high CS. (*C*) The cumulative 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 birdwatching 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.).

1. Austin J, Dezenski E, Affolter-Caine B (2008) *The Vital Connection: Reclaiming the Great Lakes Economic Leadership in the Bi-National US-Canadian Region.* (Metropolitan Policy Program, The Brookings Institution, Washington, DC).
2. Vaccaro L, Read J (2011) *Vital to Our Nation's Economy: Great Lakes Jobs Report* (Michigan Sea Grant). Available at http://www.miseagrant.umich.edu/downloads/economy/11-203-Great-Lakes-Jobs-report.pdf. Accessed October 2011.
3. Southwick Associates (2007) *Sportfishing in America: An Economic Engine and Conservation Powerhouse* (American Sportfishing Association). Available at http://www.southwickassociates.com/wp-content/uploads/2011/10/sportfishiginamerica_2007.pdf. Accessed October 2011.
4. Great Lakes Restoration Initiative Task Force (2011) Great Lakes Restoration Initiative. Available at http://greatlakesrestoration.us/. Accessed September 2010.
5. Murray C, Songhen B (2001) Valuing water quality advisories and beach amenities in the Great Lakes. *Water Resour Res* 37(10):2583–2590.
6. Bernhardt ES, et al. (2007) Restoring rivers one reach at a time: Results from a survey of U.S. river restoration practitioners. *Restor Ecol* 15(3):482–493.
7. Vörösmarty CJ, et al. (2010) Global threats to human water security and river biodiversity. *Nature* 467(7315):555–561.
8. Halpern BS, et al. (2008) A global map of human impact on marine ecosystems. *Science* 319(5865):948–952.
9. Kareiva P, Tallis H, Ricketts TH, Daily GC, Polasky S (2011) *Natural Capital: Theory and Practice of Mapping Ecosystem Services* (Oxford Univ Press, New York).
10. White C, Halpern BS, Kappel CV (2012) Ecosystem service tradeoff analysis reveals the value of marine spatial planning for multiple ocean uses. *Proc Natl Acad Sci USA* 109(12):4696–4701.
11. Austin JC, Anderson S, Courant PN, Litan RE (2007) *Healthy Waters, Strong Economy: The Benefits of Restoring the Great Lakes Ecosystem* (Great Lakes Economic Initiative, The Brookings Institution, Washington, DC).
12. Evans MC, Possingham HP, Wilson KA (2011) What to do in the face of multiple threats? Incorporating dependencies within a return on investment framework for conservation. *Divers Distrib* 17(3):437–450.
13. Millenium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Wetlands and Water-Synthesis* (World Resources Institute, Washington, DC).
14. Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011) Restoration of ecosystem services and biodiversity: Conflicts and opportunities. *Trends Ecol Evol* 26(10):541–549.
15. Vadeboncoeur Y, McIntyre PB, Zanden MJV (2011) Borders of biodiversity: Life at the edge of the world's large lakes. *Bioscience* 61(7):526–537.
16. US Environmental Protection Agency (2012) *Great Lakes Areas of Concern*. Available at http://www.epa.gov/greatlakes/aoc/. Accessed January 10, 2012.
17. Nevers MB, Whitman RL (2010) Policies and practices of beach monitoring in the Great Lakes, USA: A critical review. *J Environ Monit* 12(3):581–590.
18. Johnson JE, DeWitt SP, Gonder DJA (2010) Mass-marking reveals emerging self regulation of the Chinook salmon population in Lake Huron. *N Am J Fish Manage* 30(2): 518–529.
19. Olmstead SM (2010) The economics of water quality. *Rev Environ Econ Policy* 4(1): 44–62.
20. Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol Lett* 11(12):1304–1315.
21. Darling ES, Côté IM (2008) Quantifying the evidence for ecological synergies. *Ecol Lett* 11(12):1278–1286.
22. Barbiero RP, Lesht BM, Warren G (2011) Evidence for bottom-up control of recent changes in the pelagic food web of Lake Huron. *J Great Lakes Res* 37(1):78–85.
23. Halpern BS, et al. (2009) Mapping cumulative human impacts to California Current marine ecosystems. *Conserv Lett* 2(3):138–148.
24. Neslo R, et al. (2009) Modeling stakeholder preferences with probabilistic inversion: Application to prioritizing marine ecosystem vulnerabilities. *Real-Time and Deliberative Decision Making*, eds Linkov I, Ferguson E, Magar VS (Springer, The Netherlands), pp 265–284.
25. R Development Core Team (2010) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria).