



Metrics of ecosystem status for large aquatic systems – A global comparison

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ARTICLE INFO

Article history:

Received 1 May 2009

Accepted 28 September 2009

Communicated by Gary L. Fahnenstiel

Index words:

Metrics
Ecosystem health
Laurentian Great Lakes
African Great Lakes
Lake Baikal
Baltic Sea

ABSTRACT

We identified an objective set of 25 commonly available ecosystem metrics applicable across the world's large continental freshwater and brackish aquatic ecosystem. These metrics measure trophic structure, exploited species, habitat alteration, and catchment changes. We used long-term trends in these metrics as indicators of perturbations that represent an ecosystem not in homeostasis. We defined a healthy ecosystem as being in a homeostatic state; therefore, ecosystems with many changing trends were defined as more disturbed than ecosystems with fewer changing trends. Healthy ecosystems (lakes Baikal, Superior, and Tanganyika) were large, deep lakes in relatively unpopulated areas with no signs of eutrophication and no changes to their trophic structure. Disturbed ecosystems (lakes Michigan, Ontario, and Victoria) had shallow to moderately deep basins with high watershed population pressure and intense agricultural and residential land use. Transitioning systems had widely varying trends and faced increasing anthropogenic pressures. Standardized methodologies for capturing data could improve our understanding of the current state of these ecosystems and allow for comparisons of the response of large aquatic ecosystems to local and global stressors thereby providing more reliable insights into future changes in ecosystem health.

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Introduction

Large aquatic systems, by virtue of their size, provide important ecosystem services to human populations. These ecosystem services, along with the natural resources that support them, are being altered by human activities in ways that we have yet to understand and find difficult to predict. However, the results of losing key services such as clean drinking water or commercially important fish populations are clear in terms of human well-being. Natural resource management has responded by altering its focus from single species to the entire ecosystem which supports the species or service of interest. Within the last decade, many management agencies have incorporated a stated objective to manage for ecosystem health as a way of ensuring the sustainability of ecosystem services. The objective of maintaining ecosystem health, in turn requires measurable indicators of health.

Ecosystem health is often defined as analogous to human health (Costanza et al., 1992) because its intuitive nature aids communicating ecosystem status to the public (Lackey, 2001; Ryder, 1990).

Researchers and natural resource managers require an operational definition if they are to apply the concept and report its status, resulting in numerous attempts to define ecosystem health. Costanza et al. (1992) defined a healthy ecosystem as being stable and sustainable, with resilience to stress that allows it to maintain its organization. Rapport et al. (1998) expand on this definition with the additional requirement that a healthy ecosystem is capable of sustaining economic activity and human health while maintaining its organization. The status of the human-derived ecosystem benefits and services is a critical factor in most assessments of ecosystem health (Cairns and Pratt, 1995; Karr and Chu, 1999).

Human activities are responsible for most of the physical, chemical, and biological stresses affecting ecosystem health (Vitousek et al., 1997). However, natural conditions, such as climate variability, can cause stress and so ecosystems are responding to natural and anthropogenic stress simultaneously. Because ecosystems are changing continuously to daily and seasonal environmental forces, the limited frequency of measurement of responses in short-lived organisms may fail to identify possible stressors. Fish communities, with their longer-lived species, may be expected to integrate the effect of short- and longer-term stresses and should serve as effective metrics. Changes in fish assemblages are commonly used to evaluate

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aquatic ecosystem stress including (a) dominance of small, short-lived fish over large, long-lived fish; (b) fluctuating abundance and age within fish populations; (c) dominance of species that prefer less-structured open-water environments; and (d) higher population abundances of unexploited species (Rappport et al., 1998). Fisheries are generally an exploited resource especially in large aquatic ecosystems and therefore there is generally monitoring data available.

The size and complexity of large aquatic ecosystems dictates the need to measure numerous inputs and outputs, examine connections between many components, and identify changes in a multitude of functions and services. Measuring every essential element is not practical, so identifying a subset of metrics as a proxy of ecosystem status or health is needed (Costanza et al., 1992; Patil et al., 2001; Schaeffer et al., 1988). Such metrics or indicators can reduce enormous amounts of information into measures of the critical processes that convey ecosystem status (Niemeijer, 2002). Researchers have employed indicators or metrics in various ways to describe the health status of an ecosystem for some time. Some have used a subset of measures identified as key to a specific ecosystem (Danz et al., 2007; Reynoldson, 1993; Shear et al., 2003), whereas others have identified the common responses to stresses that indicate the degree of disturbance in any ecosystem (Odum, 1985; Rappport et al., 1985). Biomarkers have also seen increasing use as indicators of ecosystem stress (Broeg and Lehtonen, 2006).

A metric is a direct quantitative measure of an element or function. An indicator is a direct measure that also implies the status of a condition it does not directly measure (Daan, 2005). Metrics and indicators have been used to determine the status and trends of ecosystem processes and resources (Bertram et al., 2003), to provide early warnings or to diagnose the cause of environmental change (Dale and Beyeler, 2001), and to forecast future changes or direct restoration activities (Niemi and McDonald, 2004). Using a subset of validated and informative measures to represent ecosystem status allows for practical and economical monitoring efforts. Meaningful metrics and indicators are also valuable means of easily communicating the state of an ecosystem to the public (Degnbøl 2005; Niemi and McDonald 2004; Schiller et al., 2001).

Metrics and indicators have been developed and applied worldwide as measures of ecosystem health. In the Laurentian Great Lakes, a group of experts identified 80 basin-wide indicators that describe the state of the environment and measure the effectiveness of management activities (Bertram et al., 1999; Neilson et al., 2003; Shear et al., 2003). The European Union Water Framework Directive, focused on the evaluation of the ecological state of aquatic ecosystems, is based on a comparison to the undisturbed reference state of each type of ecosystem (Moss et al., 2003). This initiative examines geological and geomorphological factors, physical and chemical factors, and ecological variables as indicators of ecosystem stress. Indicators have also been used as measures of sustainable development in Europe's Lake Ladoga (Kondratyev et al., 2002). An ecosystem health index composed of 6 metrics was estimated for 8 spatial units within Moreton Bay, Australia, to demonstrate how management objectives can be incorporated into a health assessment model (Pantus and Dennison, 2005). Other researchers have used categories of metrics or indicators including biotic condition, chemical and physical characteristics, ecological processes, and disturbance (e.g., Gascuel et al., 2005; Harwell et al., 1999; Hershner et al., 2007; McNaught, 1982; Reynoldson and Metcalfe-Smith, 1992).

The objectives of this study were to select a set of metrics that could be used to examine the similarities and differences among large freshwater and brackish aquatic ecosystems worldwide and use these metrics as a measure of ecosystem status. The ecosystems we evaluated were the Laurentian Great Lakes, the African Great Lakes, Lake Baikal, and the Baltic Sea. We examined large aquatic ecosystems because their size makes them less sensitive to local effects than smaller lakes, and because they support important fisheries that

provide substantial economic value to humans and ecological importance to the ecosystems. Further, large aquatic ecosystems are often relatively well monitored because of their size and international importance. Problems detected in large lakes will likely also be impacting nearby smaller lakes to some extent, making large lakes good integrators of environmental stress and a possible early warning signal. Because these ecosystems cover a broad range of climates, geologic histories, and biogeographic domains, our metrics cannot be species-based. Consequently, these global systems with their varied histories of anthropogenic impact provide a good test of whether the chosen metrics can provide a useful evaluation of the ecosystem status and general health of these systems.

Methods

Metric selection

We conducted a workshop consisting of 15 researchers drawn from around the world with expertise in one or more of the earth's large, continental freshwater aquatic ecosystems, thereby excluding fully marine systems or marine dominated aquatic systems. We selected metrics based on three criteria: (1) the metric was representative of changes in the fish community or would be expected to impact fish communities, (2) the metric applied to all large aquatic ecosystems, and (3) data for the metrics were most likely available. There were 39 key issues identified that were used to build a metrics matrix form (Appendix A). Workshop participants used this form to summarize historical and current ranges for each metric and designate the trend (Appendix A). Additional experts were contacted to address missing values within an ecosystem or to complete a matrix for an ecosystem that lacked adequate representation at the workshop.

Before analyzing the results, we reviewed the metric matrices across all ecosystems and removed metrics that (1) had less than 50% response rate, (2) were highly correlated with another metric, and (3) did not require a trend response but were designed to capture supporting information such as lake area and maximum depth. These last mentioned metrics were important for interpreting the results. Following this review, 25 of the 39 original metrics remained (Appendix A). These metrics were classified into four categories: Trophic Structure describing changes in community level trophic interactions; Exploited Species including metrics specific to commercially harvested fish species; Habitat Alteration covering a wide range of aquatic habitat features that can impact fish communities and contains the largest number of metrics; and Catchment Change describing the human impact on the ecosystem using metrics that focus on anthropogenic pressures within the watershed.

Participants completing a matrix were asked to provide data ranges covering the past 30 years (1975–2005), or for the longest timeframe (<30 years) for which data were available. Associated metric trends were designated as increasing over time, no change, or decreasing over time. In several instances, participants were unable to provide data values for a metric but had sufficient knowledge of their systems to indicate the trend in that metric. Thus, in some cases, we obtained the expert's perception of the trend rather than empirical data. Where data were missing, we searched the literature in an attempt to complete the missing metric values.

The aquatic ecosystems represented by a metrics matrix included the Laurentian Great Lakes (Superior, Michigan, Huron, Erie, and Ontario), the African Great Lakes (Victoria [littoral, 0–6 m; sublittoral, 6–20 m], Tanganyika, and Malawi [southern basin]), Lake Baikal, and the Baltic North (Gulf of Bothnia) and Baltic Proper (Baltic Proper and Gulf of Finland) (Table 1). These aquatic ecosystems were then grouped into regions – boreal, temperate, or tropical – based on geographic location to examine possible interactions of metric responses with climatic settings, e.g., to determine whether tropical

Table 1
Ecosystem attributes and region designation.

Regions:	Boreal		Temperate					Tropical		
Ecosystems:	Baltic Sea	Baikal	Superior	Michigan	Huron	Erie	Ontario	Victoria	Tanganyika	Malawi
Population (million)	85	5	0.6	9.3	3.1	11.9	8.1	39	8.7	7.7
Lake area (km ²)	415,000	31,500	82,100	57,750	59,800	25,800	19,000	68,800	32,600	29,500
Lake drainage (km ²)	1,700,000	560,000	128,000	118,100	134,000	61,000	64,000	195,000	220,000	100,500
Volume (km ³)	21,547	23,600	12,230	4920	3537	483	1637	2760	18,900	7775
Shoreline length (km)	8000	2000	4387	2636	6159	1402	1146	3440	1828	245
Mean depth (m)	53	740	149	85	59	19	86	40	580	264
Maximum depth (m)	459	1741	407	282	229	64	245	79	1470	700
Residence time (y)	30	350	107	59	16.4	2.2	6.7	23	440	114
Age (10 ³ y)	15	30,000	10	10	10	10	10	400	12,000	2000

Attributes are shown for an entire ecosystem so subdivided ecosystems share the same attributes. Temperate and tropical attributes including lake area, lake drainage, volume, mean depth, maximum depth, and residence time are from Bootsma and Hecky (2003). Temperate ecosystems shoreline length and population data are from Canada and USEPA GLNPO (1995). Tropical lakes population data are from Nelson (2009). Lake Baikal information data are from ILEC (2009). Baltic Sea morphometric data are from HELCOM (2009) and population data are from Rikkinen (1980).

lakes are more or less sensitive to environmental disturbance. We chose metrics that would be comparable across the selected ecosystems (i.e., not taxonomically based since faunas and floras differ at these geographic scales) and examined each system from a broad, lake-wide perspective rather than focusing on localized phenomena (harbors, urbanized coastlines, etc.). As such, the data we captured do not reflect the status of every embayment or basin within an ecosystem nor do they characterize trajectories of individual species. Rather, the results are generalized to the entire ecosystem with a likely bias to the offshore pelagic realms of these large systems.

Subdividing Lake Victoria into littoral (0–6 m) and sub-littoral (6–20 m) regions violated our desire to generalize at the whole lake level. However, the shallowest region of Lake Victoria is quite extensive because of its convoluted shoreline and experiences intense use by the riparian populations. These two regions also support unique fish communities. The deeper (>20 m) regions of the lake are poorly represented in fishery data because of limited access to the canoe-based fishery, so deep offshore lake conditions are not well described. Similarly, extensive historical data were only available for the relatively shallow (<100 m depth) but extensive southern end of Lake Malawi, where the commercial fishery is located. We recognized that data from this long, deep, relatively narrow rift valley lake were highly biased to a specific portion of the lake.

We included the Baltic Sea as it functionally and spatially resembles a great lake, and its salinity does not affect the processes we examined. To save space in our presentation of results and discussion, we will refer to these Baltic systems as “lakes.” However, the unusual type of water exchange with the North Sea highlights several special features that differ from lakes (Gustafsson and Andersson, 2001). The Baltic Sea is the largest system in our analysis and we have divided it into sub-basins based on salinity conditions with the Baltic Proper being more saline (5–15%) than the Gulf of Bothnia (2–6%).

Metric analysis

As used here, metrics have values and trends. Because values may represent ecosystem-specific conditions (e.g., high species diversity in some of the systems), we used the trends, generally covering several decades, as an indicator of change in an ecosystem. Assuming all trends indicate a response to stress (or relief of a stress), and therefore a deviation from a possibly more homeostatic (healthy) state, the sum of the increasing and decreasing trends was used to represent the total amount of change in an ecosystem.

We conducted several analyses to explore characteristics of the metric trends across ecosystems. First, we employed ² analyses to examine the behavior of the metrics to ensure there were sufficient

contrasts among the ecosystems. Next, to understand how metric trends compared across ecosystems, we performed paired comparisons. For each pair of ecosystems, we tallied the matching trends shared by the pair and designated the pair as occupying the same region (within-region) or different regions (across-region). To determine if the amount of change within regions was similar, we used analysis of variance to compare the number of matched trends for within-region pairs. To determine if geographically close ecosystems are more similar to each other than to distant ones, we used analysis of variance to compare the total matches of within-region pairs to across-region pairs.

Determination of ecosystem status

For our purposes, we use the term “ecosystem health” to denote a stable ecosystem, as reflected by a homeostatic state over a set period of time. Such a condition of homeostasis (few or no trends) is assumed to either result from a lack of stressors or the ecosystem is resilient to the stresses endured. Of course, we cannot know from trends alone if the system is changing toward a more or less healthy state (e.g., a trend toward lower contaminant levels is toward a healthier system). We assume that, if a system exhibits a prolonged multidecadal trend, it must be responding to or recovering from one or more stressors and that at least a portion of the ecosystem may be in an unstable state. Therefore, we consider the number of changing metrics an indication of the degree of disturbance of the system during the last 30 years (1975–2005). A system undergoing more changes is likely subjected to more stressors, making it less stable and more likely to fail to provide its key processes and resources.

Based on the total number of changing trends, we classified ecosystems as healthy (50% or fewer changing trends), disturbed (>75% changing), or in transition (>50% and <75%). This classification allowed us to examine similarities and differences between ecosystems experiencing approximately the same amount of change. Similarities provide insight into common stress responses across the wide range of geographic regions in which the ecosystems reside and differences highlight which processes may be driven by local phenomena or may represent alternate responses to the same stressor.

Results

Designated metric trends by category

Of the 12 matrices that were completed, trends in 292 out of a total of 295 responses were designated. Some data on exploited species in littoral regions of Lake Victoria were not available and account for the three missing responses.

Metrics in the Trophic Structure category are based on functional groups and not specific species. Very few changing trends were noted in these metrics (Table 2). Changes to functional groups, especially those with multiple species in each group, do not necessarily change easily and thus may be responsible for the lack of trends in these metrics.

One metric in this category, the “Non-indigenous species invasion,” which measured the number of established non-indigenous species over time, increased across the Laurentian Great Lakes and the Baltic Sea but did not change in Lake Baikal or the African Great Lakes (Table 2). This latter group of non-invaded systems consists essentially of head water lakes on long rivers usually impassable at some point to navigation or upstream migration by fish, and so should be at low risk to the movement of species from one system to another. They also do not experience the same facilitation of dispersal associated with anthropogenic activities such as shipping and recreational boating, including ballast water and/or canals. The average annual rate of invasion was 1.81 and 0.50 new species per year in the Laurentian Great Lakes and the Baltic Sea, respectively (Leppkoski et al., 2002; Ricciardi, 2006).

The Exploited Species metrics measured an aggregated trend for the key commercially exploited species (Table 3). Historically, overexploitation has been an issue in all ecosystems we examined and continues to be closely monitored today. Some systems such as the Laurentian Great Lakes and Baltic Sea have extensive management programs that monitor stocks, set catch quotas, and supplement native and sport fish populations through stocking. In the African Great Lakes, fisheries management agencies primarily monitor fish populations and have more limited control over harvesting. Three key metrics emerged in this category: size range, mean age-at-harvest, and age-at-maturity (Table 2). Mean age-at-harvest was selected as an

Table 3

Key exploited species included in the trends designated in the Exploited Species category.

Ecosystem	Exploited species examined
African Great Lakes	
Lake Victoria	Nile perch, Nile tilapia, <i>Rastrineobola argentea</i>
Lake Tanganyika	<i>Lates</i> , <i>Stolothrissa tanganyicae</i> , <i>Limnothrissa miodon</i>
Lake Malawi	Chambo (<i>Oreochromis karongae</i> , <i>O. squamipinnis</i> , and <i>O. lidole</i>), haplochromines
Lake Baikal	Omul, taimen, northern pike
Baltic Sea	Cod, sprat, herring, salmon
Laurentian Great Lakes	Lake whitefish, walleye, yellow perch, Pacific salmon, lake trout

indicator of growth rate and age-at-maturity as an integrator of biotic and abiotic influences on individual growth. Fish ages are typically determined by seasonal markings of growth as those found in scale or otolith rings. These markings are less useful to determine age in tropical systems that do not experience marked seasonal changes. Therefore, size-at-maturity is often used as a substitute for age-at-maturity, and we use that unit of measure for the maturity metric in tropical systems.

Size of harvested species (mean body length) declined in 7 out of 12 ecosystems (Table 2). In Lake Victoria, the harvested mean body size of haplochromines, *Oreochromis esculentus*, and *Rastrineobola argentea* declined (Balirwa et al., 2003; Wanink, 1998; Witte et al., 1995). However, the average length of the introduced Nile perch *Lates niloticus* and Nile tilapia *Oreochromis niloticus* increased between the 1970s and the end of the 1980s (Goudswaard et al., 2002; Ogotu-Ohwayo, 2004) but may have decreased afterwards as indicated by a decline in size-at-maturity (Mkumbo et al., 2007) but experimental

Table 2

List of metrics trends by ecosystem.

Category and metric	Baltic North	Baltic Proper	Baikal	Erie	Huron	Michigan	Ontario	Superior	Victoria 0–6 m	Victoria 6–20 m	Tanganyika	Malawi
Trophic Structure												
Food chain length	0	–	0	0	0	0	0	0	0	0	0	0
Loss of functional groups	0	–	0	0	+	+	0	0	0	–	0	0
Within functional group diversity	0	0	0	0	0	0	+	0	–	–	0	0
Non-indigenous species invasion	+	+	0	+	+	+	+	+	0	0	0	0
Exploited Species												
Fisheries Intrinsic intrinsic stability	–	–	0	0	–	–	–	–	X	0	–	–
Size range	0	0	0	–	–	–	–	–	+	–	0	–
Mean age at harvest	–	0	–	0	+	+	–	+	X	–	–	–
Age at maturity	0	0	–	0	+	+	+	+	X	–	–	0
Trophic structure of catch	–	–	0	0	0	+	0	0	0	–	–	+
Stocking	0	0	n	0	+	+	+	0	n	n	n	n
Habitat Alterations												
Nutrient trends—phosphorus	0	0	0	–	–	–	–	0	+	+	0	+
Nutrient trends—nitrogen	+	–	0	+	+	+	+	+	+	+	0	+
Nutrient trends—dissolved silica	–	0	0	+	0	+	0	0	0	–	+	0
Chlorophyll range	+	+	0	+	0	–	–	0	0	+	0	+
Chlorophyll mean	+	+	+	–	0	0	–	0	+	+	0	0
Cyanobacteria blooms	+	+	+	+	0	0	0	0	+	+	0	+
Harmful algal species	+	+	0	+	0	0	0	0	0	0	0	+
Transparency	–	–	0	+	+	+	+	0	–	–	0	+
Oxygen demand	+	+	0	+	0	0	0	0	+	+	+	+
Contaminants	–	–	+	–	–	–	–	–	+	+	0	0
Fish diseases	–	–	0	+	+	+	+	0	0	0	0	0
Habitat loss	+	+	+	+	+	+	+	0	+	+	0	+
Catchment Changes												
Population pressure	+	+	+	+	+	+	+	0	+	+	+	+
Urbanization	+	+	+	+	+	+	+	+	+	+	0	+
Economic activity	+	+	+	+	–	–	–	–	+	+	+	+

Values represent the trend as “+” increasing, “–” decreasing, “0” no trend. Values designated as “n” do not apply to the ecosystem and “X” is an unknown trend.

trawl surveys conducted during the early and mid 1990s did not find changes in the mean body size of Nile perch (Kolding et al., 2008). In Lake Malawi, we did not have data by species but harvest data indicates that total catches of larger species declined along with a decline in mean size-at-harvest (Nsiku, 1999). In lakes Michigan, Huron, and Ontario, lake whitefish *Coregonus clupeaformis* growth has slowed since the early 1990s (Hoyle, 2005; Lauer et al., 2008; Mohr and Ebener 2005).

Little or no change in size of harvested species occurred in 4 ecosystems. In Lake Tanganyika, fishing pressure from early industrialization caused a shift from large species to small species resulting in a decline in the mean size of fish in the catch overall. However, most individual species did not experience a change in size-at-harvest although all *Lates* species declined in size (Coulter, 1991; Mannini et al., 1996). In Lake Baikal, there was no evidence of change in size for the major commercial species, omul *Coregonus autumnalis migratorius* (Kozhova and Izmet'eva, 1998) while the size of some recreational fish species, including taimen *Hucho taimen* and northern pike *Esox lucius*, declined (Matveyev et al., 1998; Owens and Pronin, 2000). There was little or no change in size for most commercial species in the Baltic Sea basins (ICES, 2007). However, the weight and condition of herring *Clupea harengus membras* declined during the 1990s in the Baltic Proper likely due to increasing pelagic predators and a decline in food availability (Cardinale and Arrhenius, 2000) and quality (Flinkman et al., 1998).

Mean age-at-harvest declined in the African Great Lakes, Lake Baikal, and the Baltic North. In Lake Tanganyika, although specific age data are limited, all large *Lates* species and *Stolothrissa tanganyicae* in limited areas are now caught smaller and younger than in previous years whereas ages for the clupeid *Limnothrissa* are variable with no specific trend (Coulter, 1991; Mannini et al., 1996; Mulimbwa, 2006; Sarvala et al., 1999). For Lake Malawi, there were few data on age of harvested fish, but changes in the harvest over time shifted from larger to smaller fish (Nsiku, 1999) suggesting that at least for some species, younger fish are being taken in the harvest. Similarly, there are few to no data on age-at-harvest in Lake Victoria but size of most harvested species has declined since the 1960s (Balirwa et al., 2003; Kolding et al., 2008). In Lake Baikal, omul mean age declined in the Selenga River area and in the northern lake region (Kozhova and Izmet'eva, 1998) and younger taimen have been caught since the 1980s (Matveyev et al., 1998). In the northern Baltic Sea, mean age of herring declined after the 1980s but mean age of sprat *Sprattus sprattus* remained unchanged (ICES, 2007).

In the Laurentian Great Lakes, trends in mean age-at-harvest vary by lake. Lake Erie is the only lake that has not experienced a change in mean age-at-harvest (Belore et al., 2005; Thomas and Haas, 2005). In lakes Michigan, Huron, Ontario, and Superior, mean age of lake whitefish increased (Bronte et al., 2003; Hoyle, 2005; Mohr and Ebener, 2005), possibly related to decreased growth attributed to density-dependent effects and declining abundance of the benthic amphipod *Diporeia* (Nalepa et al., 2005).

Age-at-maturity increased for many species in the Laurentian Great Lakes. In Lake Superior, age-at-maturity for lake trout increased during 1970–2003 (Sitar and He, 2006). Lake whitefish age-at-maturity increased in the lakes Huron (Mohr and Ebener, 2005), Michigan (Madenjian et al., 2006), and Ontario (Hoyle, 2005). However, not all species experienced an increase in age-at-maturity. In Lake Michigan, Chinook salmon *Oncorhynchus tshawytscha* age-at-maturity decreased from the mid 1980s to early 1990s (Peeters and Royseck, 2004) while the age-at-maturity for yellow perch *Perca flavescens* showed no trend (Doll and Lauer, 2007). No trend in age-at-maturity was seen for walleye or yellow perch in Lake Erie (Belore et al., 2005; Thomas and Haas, 2005).

In the sub-littoral regions of Lake Victoria, Nile perch size-at-maturity initially declined (no data for littoral areas) followed by an

increase during the 1970s and a subsequent decrease beginning in the 1980s (Kolding et al., 2008; Ogutu-Othwayo, 2004). Size-at-maturity declined for *R. argentea* and several of the sub-littoral haplochromines after the 1970s and for *O. niloticus* in the early 1990s (Kolding et al., 2008; Njiru et al., 2006; Wanink, 1998; Witte et al., 1995). In Lake Tanganyika, there are limited data on change in size-at-maturity for most species but *Lates mariae* age-at-maturity has likely decreased (Coulter, 1991; Mannini et al., 1996). Data on size-at-maturity for most species were not available for Lake Malawi, Lake Baikal, or the Baltic Sea. We assumed no trend for this metric except in Lake Baikal where reductions in mean age-at-harvest of omul may also have lead to reductions in age at maturity (Kozhova and Izmet'eva, 1998).

The Habitat Alterations category had the largest number of metrics and included a wide range of aquatic habitat variables. Changes in water chemistry, captured by metrics on phosphorus (P), nitrogen (N), and silica (Si) levels, have occurred in all ecosystems (Table 2). In the Laurentian Great Lakes, phosphorus concentrations declined in all lakes except perhaps Superior, whose P concentrations remained below target levels, following the establishment of the Great Lakes Water Quality Agreement in 1972 (IJC, 1978; Neilsen et al., 2003). In Lake Victoria, P levels have increased due to increased population and associated land use practices including slash and burn agriculture which have resulted in eutrophication of both the littoral and sub-littoral areas (Hecky, 1993; Verschuren et al., 2002). Similar land use practices have increased P levels and eutrophication in Lake Malawi (Hecky et al., 2003), although P levels remain below those in Lake Victoria (Guildford and Hecky, 2000). Lake Tanganyika's mountainous shorelines have limited agricultural land use and kept P levels low and without trend (Bootsma and Hecky, 2003). Although P levels increased dramatically in the Baltic Sea during the 20th century, they remained stable or slightly decreased during the last decade (Elmgren, 2001; Fleming-Lehtinen et al., 2008b).

Nitrogen concentration showed no trend in Lake Baikal, Lake Tanganyika, and the Baltic Proper (Table 2). Across the Laurentian Great Lakes, nitrogen concentration increased (Holland et al., 1995; Neilson et al., 2003), especially in Lake Superior where nitrate levels increased 5-fold in one century (Sterner et al., 2007). Lake Victoria experienced increasing total nitrogen concentrations in the littoral and sub-littoral regions attributed to agricultural runoff, sewage outflows, re-mineralization processes, and N-fixation by cyanobacteria (Hecky, 1993; Lung'ayia et al., 2001). Lake Malawi has also experienced increasing nitrogen inputs associated with increasing human populations and land use changes (Hecky et al., 2003). Changes in nitrogen concentration varied in the Baltic Sea where levels were stable in the Baltic Proper (HELCOM, 2008; Rahm and Danielsson, 2007) but increased in the northernmost Baltic between the 1980s and 2000s (Olsonen, 2007).

Trends in silica concentration were not observed in many ecosystems. Multidecadal increases were observed in lakes Erie (Rockwell et al., 2005), Michigan (Barbiero et al., 2002; Johengen et al., 1994), and Tanganyika (Verburg et al., 2003, 2006). Although higher silica concentrations have been observed near river mouths in Lake Victoria (Lung'ayia et al., 2001), silica concentration decreased in the sub-littoral areas where high burial losses were caused by excess diatom production (Hecky, 1993; Verschuren et al., 2002). Silica concentration also decreased in the northern Baltic Sea between 1970 and late 1990s (Fleming-Lehtinen et al., 2008b).

Cyanobacteria blooms have increased in Lake Erie accompanied by a resurgence of *Microcystis* spp., likely related to an increase in nutrients or selective filtering by *Dreissena* spp. mussels (Conroy et al., 2005). Blooms have also become increasingly common especially in the littoral areas of Lake Victoria (Verschuren et al., 2002) and Lake Malawi (Andre et al., 2003). Although cyanobacteria blooms

are not frequent in Lake Baikal, their incidence has increased in the past few decades and is thought to be related to increasing, but still low, local eutrophication (Tarasova et al., 2006). Research on sediment cores in the Baltic Sea suggest that the blooms have been occurring since the Littorina Sea stage (ca. 7000–4000 BP) and may be a normal state (Bianchi et al., 2000). However, the frequency and intensity of blooms has increased since the 1960s (Vahtera et al., 2007).

The contaminant metric summarized all types of chemical pollutants into a general trend. Although there are some indications of pollutants in lakes Tanganyika and Malawi, there was no indication of a trend in either lake (Chale, 2002; Karlsson et al., 2000; Kidd et al., 2003). In Lake Victoria, mercury concentrations (Campbell et al., 2003a,b) and raw or incompletely treated effluents (Lung'ayia et al., 2001) are increasing although levels of mercury and organochlorine pesticide residues in the lake's fish are currently low (Campbell et al., 2003a; Kasozi et al., 2006). Primary contaminants in Lake Baikal were oil-based products, phenol compounds and metals (Kozhova and Silow, 1998) and effluents from gold mining operations on the Selenga River, important taimen spawning habitat (Stubblefield et al., 2005). Extensive contaminant reduction programs established in the Laurentian Great Lakes (Charlton et al., 1993; Marvin et al., 2003; Neilsen et al., 2003) and the Baltic Sea (Olsonen, 2007; Wulff et al., 2001) have generally reduced “legacy” contaminants in these systems although concerns continue about emerging contaminants.

The transparency metric was measured using Secchi depth. Secchi depths in lakes Tanganyika and Baikal showed no trend and averaged more than 12 m (Chale, 2004; Hampton et al., 2008; Langenberg et al., 2002; Sarvala et al., 2006b). Except for the consistently oligotrophic Lake Superior, Secchi depth increased in all other Laurentian Great Lakes in association with phosphorus abatement programs and filtering by invasive dreissenid mussels (Binding et al., 2007; Charlton et al., 1999; Dobiesz and Lester 2009). Transparency increased in Lake Malawi (Guildford et al., 2007; North et al., 2007) but decreased in Lake Victoria with the lowest transparency in the littoral areas associated with increasing eutrophication (Lung'ayia et al., 2001). Anthropogenic activities have increased eutrophication in the Baltic Sea where Secchi depth decreased by 0.05 m/y from 1969 to 1991 (Fleming-Lehtinen et al., 2008a; Sanden and Hkansson, 1996).

Oxygen demand did not change in Lake Baikal (Kozhova and Silow, 1998) or the Laurentian Great Lakes, except in Lake Erie where hypoxia, once limited to selected areas, has become more widespread (Burns et al., 2005). In the Baltic North, oxygen availability fell slightly between the 1960s and 2000s but is still sufficient to support benthic organisms whereas hypoxia and anoxia are more prevalent in the Baltic Proper (Olsonen, 2007). Across the African Great Lakes, anoxic conditions are associated with the bottom waters due to the stability of the water column (Coulter et al., 1986). Plant decomposition and increasing stability of the water column associated with global warming have resulted in shallower oxyclines in the African lakes (Hecky et al., 1994; Lung'ayia et al., 2001; Verburg et al., 2003).

The fish disease metric summarizes the changes in the incidence of all fish diseases into a single trend. Very little is known about the incidence of fish diseases in the African Great Lakes but workshop participants believed it is low (J. Sarvala and F. Witte, unpublished data). In contrast, fish diseases across the Laurentian Great Lakes, except in Lake Superior, have occurred with increasing frequency (SOLEC, 2007). In the Baltic Sea, Salmon M-74 fry mortality syndrome temporarily increased in the 1990s then decreased during the 2000s to its present low level (<10%) (ICES, 2006).

Habitat loss increased in all aquatic ecosystems except lakes Tanganyika and Superior, which are generally less impacted by anthropogenic activities within their watersheds (Bronte et al.,

2003; Mannini, 1998). However, erosion in Lake Tanganyika's watershed has increased siltation with negative impacts on the species that favor rocky habitat (Cohen et al. 1993). In the Laurentian Great Lakes (excluding Lake Superior), habitat loss has occurred due to various human activities including dam building, shoreline development, contaminants such as fertilizers, pesticides, petrochemical exploration, and development, and leaking septic tanks (SOLEC, 1995; Webb, 2008). In Lake Baikal, expanding grazing activity, loss of flood plain habitat, and gold mining practices all increase suspended sediments that threaten the spawning habitat of taimen, lenok, and sturgeon (Matveyev et al., 1998). In the Baltic Sea, salmon spawning rivers decreased in numbers from 44 to 12 due to dam construction while herring spawning grounds in the Baltic North (Bothnian Sea) have deteriorated due to a decrease in *Fucus vesiculosus* algae and an increase in filamentous algae and degraded coastal habitats caused by cultural eutrophication (HELCOM, 1996; ICES, 2006). The same habitat losses have occurred in the Baltic Proper, but in addition, nursery habitats have been reduced as eutrophication, dredging, and boat traffic have altered macrophyte species composition (Eriksson et al., 2004; Munsterhjelm, 1997).

The highest percentage of increasing trends occurred in the Catchment Change category (Table 2). Population pressure was increasing in every ecosystem except Lake Superior (Sousounis and Albercook, 2000). In Lake Victoria's catchment, human population density has steadily increased since the 1960s at a rate of more than 3% per annum, while somewhat slower rates of increase occurred in lakes Malawi and Tanganyika (Allison, 2002; Bootsma and Hecky, 1993). Increasing urbanization impacted all ecosystems (Bootsma and Hecky, 1993; Canada and USEPA GLNPO, 1995; Rikkinen, 1980) except Lake Tanganyika (Bootsma and Hecky, 1993). Areas outside of North America experienced increasing economic activity (Allison, 2002; Kozhova and Silow, 1998) while slowing economic growth in the US Midwest accounted for a decline in economic activity in the Laurentian Great Lakes watershed (BEA, 2005).

Analyses of trends by ecosystem and region

Across all ecosystems, more trends were changing than not ($\chi^2 = 14.92$, $p < 0.01$, $n = 292$), but the total amount of change varied by system (Fig. 1). Lakes Tanganyika, Superior, and Baikal had the

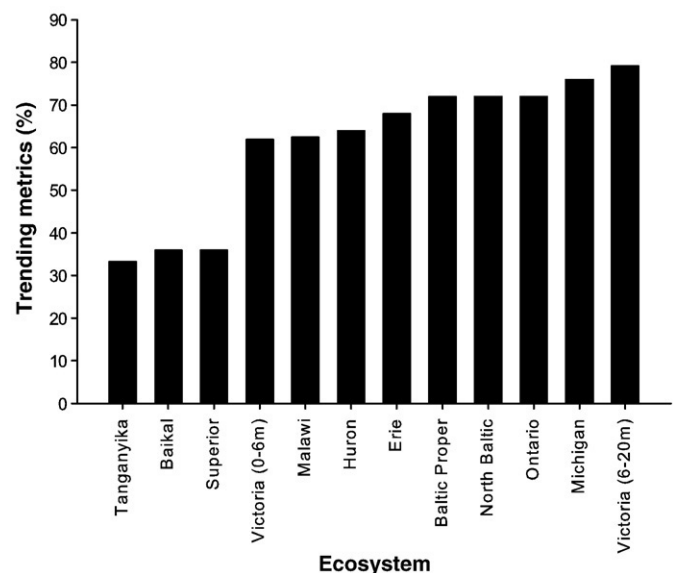


Fig. 1. Total number of trending metrics (out of a total of 25 metrics) by ecosystem.

fewest changing metrics, which is consistent with the general perception that these lakes have been the least impacted by anthropogenic activities (Bronte et al., 2003; Coulter et al., 1986; Environment Canada and U.S. EPA, 2007; Kozhova and Izmet'seva, 1998). In contrast, lakes Michigan, Ontario, and Victoria, and both segments of the Baltic Sea had the highest number of changing metrics (Fig. 1) and are generally thought to be systems that have experienced substantial ecosystem change, for better or worse (Elmgren, 2001; Madenjian et al., 2002; Mills et al., 2003; Verschuren et al., 2002).

Similar amounts of change are occurring in each region ($F=1.1$, $df=2,16$, $p=0.388$) inferring that the selected metrics do not emphasize changes in any particular region. Ecosystems within each region are more similar to each other than to ecosystems in other regions ($F=29.88$, $df=1,64$, $p=0.001$). On average, ecosystems within a region have 14 matching trends, whereas ecosystems across two regions have only 10 matching trends. Therefore, geographically close ecosystems have more in common with each other than with systems in other regions. The number of changing metric trends varied by category. A higher number of trends were changing in Exploited Species ($\chi^2=5.06$, $p=0.024$), Habitat Alteration ($\chi^2=8.03$, $p=0.005$), and Catchment Change ($\chi^2=28.44$, $p<0.001$) categories, whereas non-changing metrics dominated the Trophic Structure category ($\chi^2=6.75$, $p=0.009$). On average, over 90% of the anthropogenic stressors in all watersheds were in flux.

The number of changing trends in each category was summed, and the percent of changing metrics produced patterns of change within regions showing the similarities and differences between geographically close ecosystems (Fig. 2). In the temperate region, all lakes except for Lake Erie show a similar pattern (Fig. 2). Similarly, in the tropical region, both segments of Lake Victoria have similar patterns of change that differ from the patterns of

Table 4

Summary of trending metrics for each aquatic system and designated ecosystem health status.

Ecosystem	Number of changing metrics	Total number of metrics trends designated	Percent of changing metrics	Health status
Tanganyika	8	24	33	Healthy
Superior	9	25	36	Healthy
Baikal	9	24	38	Healthy
Victoria, littoral	13	21	62	Transitioning
Malawi	15	24	63	Transitioning
Huron	16	25	64	Transitioning
Erie	17	25	68	Transitioning
Baltic North	18	25	72	Transitioning
Baltic Proper	18	25	72	Transitioning
Ontario	18	25	72	Transitioning*
Michigan	19	25	76	Disturbed
Victoria, sub-littoral	19	24	79	Disturbed

Because of the high proportion of matching trends shared by Lakes Ontario and Michigan, we describe Lake Ontario in the section on “disturbed” ecosystems.

lakes Tanganyika and Malawi (Fig. 2). In these geographic regions, the shallower lakes Erie and Victoria are experiencing different changing metrics than the nearby, deeper lakes. Trends by category were similar across the two segments within Lake Victoria (Fig. 2) which are divided by depth. This physical subdivision does not impose a barrier to exchange of mobile biota or water. In contrast, trends by category differed between the two basins in the Baltic Sea that are subdivided by a stable variation in salinity (Ojaveer and Lehtonen, 2001) (Fig. 2). Although also in the boreal region, Lake Baikal did not match the patterns in the Baltic Sea (Fig. 2). A number of different environmental features in this ecosystem including Baikal's isolation and low population density are likely explanatory factors.

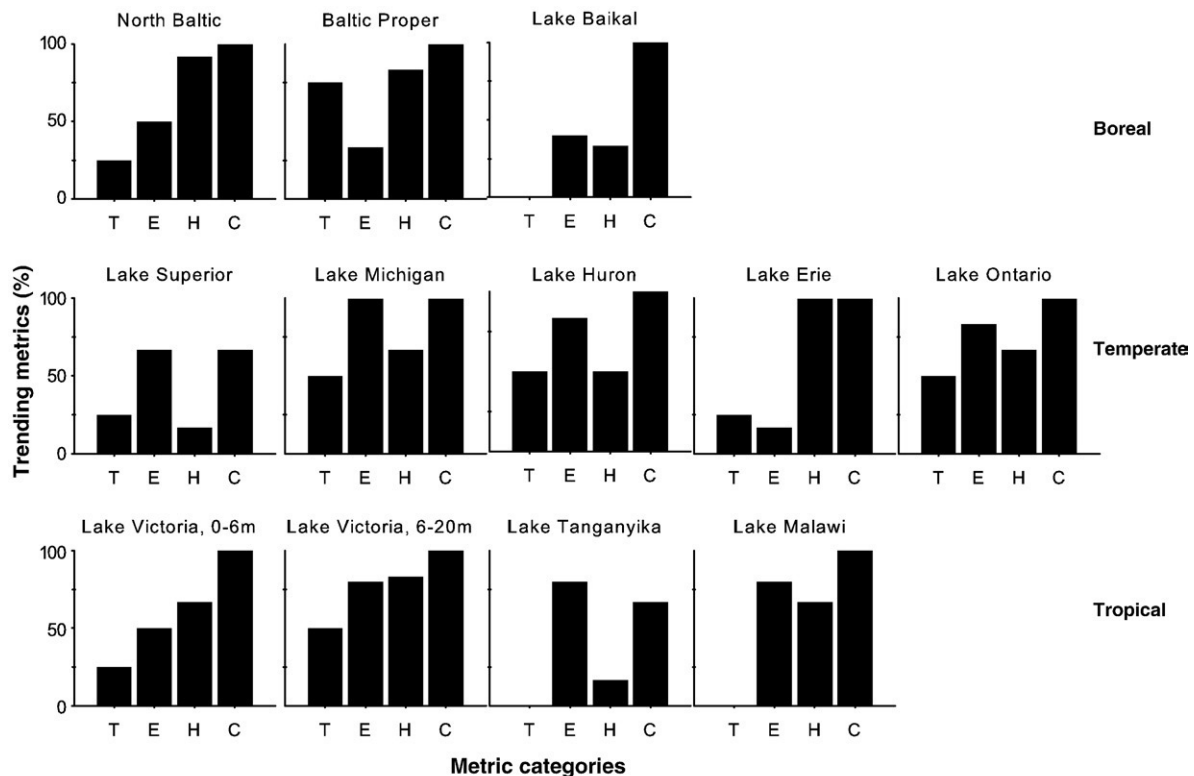


Fig. 2. Percent of changing metrics in each metric category (T=Trophic Structure, E=Exploited Species, H=Habitat Alteration, C=Catchment Changes) for each ecosystem arranged by geographical region.

Ecosystems designated as “healthy”

Based on our health classification, lakes Baikal, Superior, and Tanganyika were designated as healthy (Table 4). These ecosystems shared six non-trending metrics including chlorophyll range, transparency, fish disease, phosphorus levels, loss of functional groups, and within functional group diversity (Table 2). These metrics represent habitat alterations and trophic structure changes; there were no common trends in metrics measuring exploited species or catchment changes. However, each of these ecosystems had one or more signs of increased anthropogenic effects (population pressure, urbanization, and economic activity) and trending exploitation metrics.

The healthy ecosystems differ in several fundamental ways. Biodiversity ranges from 52 native fish species in Lake Baikal (Kozhova and Izmet'eva, 1998) to 83 in Lake Superior (Coon, 1999) and 325 in Lake Tanganyika (Snoeks, 2000). The different biophysical regions in which the ecosystems exist drive abiotic factors such as temperature and precipitation. Some differences

represent responses to regional or local stressors. For instance, the hydraulically connected Laurentian Great Lakes and the economically important shipping industry facilitate the invasion and spread of non-native species throughout the lakes (Grigorovich et al., 2003) resulting in an invasion rate of 1.81 species per year across the Laurentian Great Lakes (Ricciardi, 2006). Such dispersal mechanisms are very limited to non-existent in lakes Baikal and Tanganyika.

Contaminant trends varied among the healthy ecosystems highlighting local differences in land use and environmental protection efforts. Within the past 40 years, the human population around Lake Baikal has tripled, agricultural and forestry land uses have increased, and capital investment has grown 22 times leading to an increase in major pollutants entering the lake (Kozhova and Silow, 1998). In Lake Tanganyika, there were no trends in contaminants in the water but some studies indicate heavy metals are accumulating in several fish species (Campbell et al., 2008; Chale 2002). In Lake Superior, strict environmental programs reduced most contaminants, except for toxaphene, which remains at levels

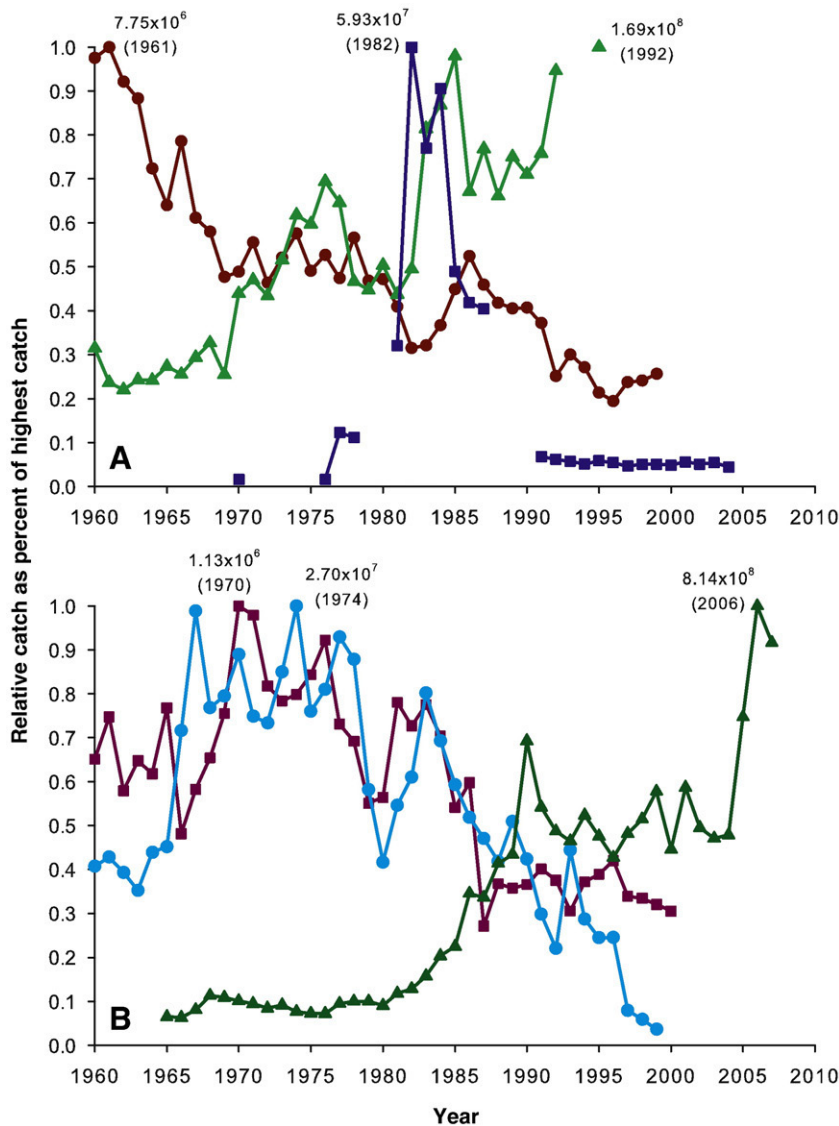


Fig. 3. Relative commercial catch (annual proportion of highest year) in ecosystems designated as (A) healthy [Lake Superior (open circle), Lake Tanganyika (solid triangle), and Baikal (solid square)] and (B) disturbed [Michigan (open circle), Ontario (solid square), and Victoria (solid triangle)] models. For each ecosystem, maximum catch (kg) and year of occurrence is labeled.

that are higher than other Laurentian Great Lakes (Kucklick and Baker, 1998).

Relative commercial catches changed over time but patterns of change were very different among ecosystems (Fig 3A). Harvests declined in lakes Superior (Baldwin et al., 2002) and Baikal (Kozhova and Izmes'teva, 1998; Marianne Moore, Wellesley College, Wellesley, Massachusetts, personal communication) but have increased in Tanganyika (Sarvala et al., 2006a). In Lake Baikal, increased log rafting operations and pollution of spawning grounds have decreased omul (Kozhova and Silow, 1998) and taimen abundances (Matveyev et al., 1998). These impacts are also reflected in the taimen age-at-harvest which has declined from an average 8–29 years in the 1960s to 2–5 years by the 1990s (Matveyev et al., 1998). In Lake Superior, intensive efforts to manage the water quality, reduce overexploitation, and control parasitic sea lamprey have been largely responsible for the recovery of the fish community. The lake trout population, once supported through stocking, is now naturally reproducing and self-sustaining (Bronte et al., 2003). Lake whitefish stocks have largely recovered and are approaching historic levels, whereas lake herring *Coregonus artedii* stocks have also increased but experience sporadic recruitment (Bronte et al., 2003). However, overall catch remains below the historic level due to lower market prices that have reduced the number of active commercial fishers (Bronte et al., 2003).

In Lake Tanganyika, catches have remained high but species composition in the catch has fluctuated. Exploited commercial fish species are *Limnothrissa miodon*, *S. tanganyicae*, and *Lates stappersii* but the targeted species vary by location. A shift from traditional subsistence fishing to industrial lift-nets in the 1960s increased average catch efficiency from 3 to 14 tons per year by the 1990s (Coenen, 1995). Present fishing pressure is very high, especially on the larger *Lates* species (Coulter, 1976), but even the small planktivorous clupeid *S. tanganyicae* seems to be overexploited in northern Congolese waters (Mulimbwa, 2006). As harvesting intensified, a shift in catch composition from large to small fish, along with a simultaneous shift from piscivorous to zooplanktivorous fish, has been documented from the north and south ends of the lake (Kimirei et al., 2008; MIs et al., 1999). In addition to this general trend, there have been long-term fluctuations in the catch composition, clupeid dominance alternating with a dominance of *L. stappersii* (Chitamwebwa and Kimirei, 2005; Coulter, 1991; Roest, 1992; van Zwieten et al., 2002).

Ecosystems designated as “disturbed”

Two ecosystems were classified as “disturbed,” Lakes Michigan and sub-littoral Lake Victoria (Table 4). Trend similarities include a decline in size range of exploited species, possibly related to fishing intensity or food web changes, and an increase in nitrogen levels, habitat loss, population pressure, and urbanization, indicative of anthropogenic impacts. Lake Ontario also shares all of these metric trends (Table 2); but, since it had one less changing trend (18 changing trends) than either lakes Michigan or Victoria, it was designated as an ecosystem in transition by our criterion (Table 4). However, because of the high degree of similar trends shared with Lake Michigan (20 of 25 common trends), we discuss it in this section.

Many trends in lakes Michigan and Ontario have occurred in different directions from Lake Victoria. Invasive species and fish diseases have increased throughout lakes Michigan and Ontario (Koonce, 1995; Ricciardi, 2006; Wright et al., 2008) but did not increase in Lake Victoria where neither of these metrics represent current problems although fish parasites are present (Ogwai, 1994). Most contaminants declined throughout the Laurentian Great Lakes (Neilson et al., 2003) but mercury concentrations (Campbell et al.,

2003a,b) and raw or incompletely treated effluents (Lung'ayia et al., 2001) increased in Lake Victoria.

Phosphorus and chlorophyll concentrations have generally declined in lakes Michigan and Ontario along with an associated increase in transparency. Cultural eutrophication, degradation of water quality, invasion by exotic species, and overfishing contributed to a decline of native fish stocks in lake Michigan (Wells and McLain, 1973) and Ontario (Christie 1972). Phosphorus abatement programs begun in the early 1970s were largely successful and reversed the eutrophication and improved water clarity (Madenjian et al., 2002; Mills et al., 2003). In the sub-littoral region of Lake Victoria (6–20 m), primary production doubled, attributed to population growth and land use changes (Goldschmidt et al., 1993; Hecky, 1993; Hecky and Bugenyi, 1992). Algal biomass increased four to five times leading to a decline in water transparency (Verschuren et al., 2002) and diatoms have been replaced by cyanobacteria as the dominant planktonic algae (Kling et al., 2001).

Age-at-maturity increased for key exploited species in lakes Michigan and Ontario but decreased in Lake Victoria. Lake whitefish age-at-maturity increased from 3.5 in the mid-1980s to 5 years by early 2000s in Lake Michigan (Madenjian et al., 2006) and from age 4 to age 7 between 1999 and 2002 in Lake Ontario (Hoyle, 2005). Other changes in the lake whitefish population included declining body condition and size-at-age (Lumb et al., 2007; Madenjian et al., 2006). These changes have been attributed to several possible factors including adaptive responses to decreased growth rates associated with declines in *Diporeia*, the staple food of whitefish (Hoyle, 2005; Nalepa et al., 2009; Wang et al., 2008) and density-dependent mechanisms (DeBruyne et al., 2008; Kratzer et al., 2007). In Lake Michigan, mean age of yellow perch increased by approximately 3 years between 1987 and 1997 and length during this period increased from 187 mm to 203 mm (Marsden and Robillard, 2004).

In tropical lakes, size-at-maturity often replaces the measure of age-at-maturity. Size-at-maturity of the introduced Nile perch in Lake Victoria was initially lower than in lakes where they are endemic, but increased during the 1970s, then decreasing between 1980 and 2002 (Kolding et al., 2008; Ogutu-Ohwayo, 2004). Size-at-maturity has been declining for *R. argentea* since 1970s and for *O. niloticus* since early 1990s (Njiru et al., 2006; Wanink, 1998). Size-at-harvest has also declined for haplochromines and *R. argentea* but initially increased for Nile perch then declined during the latter part of the 30-year period (Balirwa, 2007; Ogutu-Ohwayo 2004; Wanink, 1998; Witte et al., 1995). *O. esculentus* size-at-harvest declined between 1920 and 1970, likely derived from the shift to smaller mesh sizes (Ogutu-Ohwayo, 1990) precipitated by declining harvest of large fish. Despite these changes, overall fish catches (biomass) have increased dramatically (Fig. 3A).

Commercial catches in lakes Michigan, Ontario, and Victoria (6–20 m) appear to be driven by metrics that they do not share in common. Since 1974, the relative commercial catches have declined in lakes Michigan and Ontario while increasing in Lake Victoria (Fig. 3B). Management activities in lakes Michigan and Ontario have made substantial progress in restoring fish communities but the efforts have not lead to sustained improvements in total commercial catch, although the lakes now support substantial recreational fisheries (Shear, 2006) that are not included here (Fig. 3B). Declining commercial catches have been attributed to poor water quality, loss of habitat, overexploitation, and negative impacts of invasive species (Hoyle, 2005; Hoyle et al., 2008; Lauer et al., 2008; Lumb et al., 2007) all of which can directly impact stocks but have also likely affected market demand because of the negative perception of the health of the lakes and historic contamination of their fish.

In Lake Victoria, declines in the tilapia fishery during the 1950s led to introductions of exotic tilapias and piscivorous Nile perch which in

turn led to a dramatic decline in haplochromines in the littoral and sub-littoral areas (Barel et al., 1985, Ogutu-Ohwayo, 1990; Witte et al., 1992). Concurrently, eutrophication increased in Lake Victoria resulting in decreased water transparency, increasing algal blooms, and declining levels of dissolved oxygen (Hecky, 1993; Hecky et al., 1994; Kaufman, 1992). Differences in trends describing primary productivity and nutrient status may help explain the diverging catches in these lakes (Fig. 3B). It should also be noted that Lake Victoria has seen increasing catches despite the large number of changing metrics which classify it as a highly disturbed system, indicating that even unhealthy ecosystems can provide important ecosystem benefits.

Ecosystems in transition

Among the six transitioning ecosystems (Table 4), metric trends varied widely, but all systems experienced increases in habitat loss, population pressure, and urbanization (Table 2). Similar to Lake Ontario, the Baltic North and Baltic Proper had 18 changing trends, just under the cutoff (75% changing metrics) for our designation as “disturbed.” However, Lake Ontario possessed more common trends with a disturbed lake, Lake Michigan, whereas the Baltic basins were more similar to each other than to the other systems. Since the basins are subdivisions of a single water body and face very similar stressors, they share 20 of 25 metric trends (Table 2). Differences in salinity, total nutrients, and primary production rates (Tamminen and Andersen, 2007) within the two basins appear to have little effect on the metrics we used.

The transitioning status for the Baltic Proper may be explained by the regime shifts that researchers believe have occurred in the ecosystem (Alheit et al., 2005; sterblom et al., 2007). The Baltic Proper has undergone at least three regime shifts: (1) a shift from seal to cod as the top predator; (2) a shift from an oligotrophic to eutrophic state; and (3) a shift in biomass from cod to sprat (sterblom et al., 2007). The first two shifts occurred before 1975 and were outside the time period of this study but may have influenced the early part of the time series. The regime shifts were not detected in the northernmost Baltic but the high number of trends shared with the Baltic Proper implies many of the same stressors were at work but did not lead to an identifiable regime shift.

The littoral region of Lake Victoria was classified as a transitioning ecosystem (Table 4). This region experienced more changing trends than the sub-littoral region but this was based on data for a single zooplanktivorous rock dwelling *Haplochromis (Pundamilia) nyererei* (Witte et al., 1992) for which we had data and may not represent the trend for the entire littoral fish community. Because we lacked data for three metrics in this segment (Table 2), it is difficult to determine whether the actual state of the littoral area.

Lakes Erie and Huron were classified as transitioning systems and shared several trends that represent local phenomena, such as the increasing incidence of fish disease (SOLEC, 2007) and decreasing contaminant levels (Neilsen et al., 2003). Habitat metric trends varied in lakes Erie and Huron, and the exploited fish community appeared to be responding to these differences (Table 2). Exploited species trends were based on the major commercial species in each ecosystem (Table 3), so variation in trends between these lakes could be attributed to differences in the key species. In Lake Erie, yellow perch and walleye *Sander vitreus* dominate the fisheries (Ryan et al., 2003), whereas lake whitefish and salmonids dominate the Lake Huron fisheries (Dobiesz et al., 2005). In Lake Erie, there was little change in the biological characteristics yellow perch and walleye between the 1980s and 2003 (Bur et al., 2005). Commercial harvest of these species has been mixed with the 2004 harvest of yellow perch the highest since 1990 (Belore et al., 2005) while in the same year the commercial harvest of walleye was the lowest since 1983 (Thomas and Haas, 2005). In Lake Huron, lake whitefish

consumption of the energetically dense *Diporeia* spp. declined by 46–96% (Pothoven and Madenjian, 2008). This change in diet has been linked to a decline in mass-at-age and condition of lake whitefish. Biomass of age-3 and older lake whitefish declined from 22 million to 8 million kg between 1993 and 2003 (Ebener et al., 2008). Walleye populations have not varied much since the 1970s (Dobiesz et al., 2005). Lake trout populations, nearly extirpated by overfishing and the parasitic sea lamprey, show signs of increasing natural reproduction in Michigan waters of the main basin (Riley et al., 2007).

There were 16 changing trends in Lake Huron, the second lowest of the Laurentian Great Lakes after Lake Superior (Table 4). We based this analysis on 1975–2005, but changes in Lake Huron after 2005 indicate a more recent possible regime shift with a return to a more historical fish community. A sequence of changes began in the early 1990s that continues to change the food web dynamics in the lake. Invasion and establishment of non-native Dreissenids reduced nutrients for the pelagic community, causing declines in plankton and amphipod (*Diporeia* spp.), which contributed to the collapse of the alewife (Bence and Mohr, 2008), a key prey fish, and to declining growth and condition of lake whitefish (Ebener et al., 2008). Chinook salmon *O. tshawytscha*, which fed almost exclusively on alewives, also experienced declines in growth and condition (Dobiesz et al., 2005). Native species, lake trout and walleye, also used alewives as a food source but have adapted to other prey species including the invasive round goby *Neogobius melanostomus*. Current increases in natural reproduction of walleye and lake trout may eventually eliminate the need for stocking (Bence and Mohr, 2008; Riley et al., 2007).

The southern basin of Lake Malawi was designated as a transitioning ecosystem, and although the maximum depth of the lake is 700 m, the southern basin is considerably shallower with a maximum depth just over 100 m (Bootsma and Hecky, 2003). This may explain, in part, why southern Lake Malawi shared more common trends with shallow Lake Erie than with the deeper Lake Huron. Increases in nitrogen levels, chlorophyll range, oxygen demand, cyanobacteria blooms, and harmful algae species occurred in both Erie and Malawi (Burns et al., 2005; Conroy et al., 2005; Guildford et al., 2007; Hecky et al., 2003; Martin et al., 1998; Neilson et al., 2003). These trends are driven, at least in part, by anthropogenic activities within the catchments.

Habitat changes in lakes Erie and Malawi were very similar but exploited species reacted somewhat differently to the trends. Unlike Lake Erie, Lake Malawi has a species-rich fish community (Barel et al., 1985; Reinthal, 1993) with a wide variety of fishing methods used to harvest these species (Nsiku, 1999). Total catches (commercial and traditional) have ranged between 50 and 70 thousand metric tons between 1976 and 1991 but declined in the early 1990s to a minimum of 30 thousand metric tons despite an increase in the number of gill nets (Weyl et al., 2001). The decline in catch and the change in species composition have been attributed to overexploitation and declining water quality (Bootsma and Hecky, 2003; Darwall, 2001). Size range of exploited species has generally declined but this trend may be, in part, related to use of mesh sizes below the legal limit (Weyl et al., 2001).

Discussion

Comparing large lake ecosystems is made difficult by the fact that they are relatively few, have had different geological and evolutionary histories, occur within different biogeographic regions, and a common set of species does not exist. During the creation of the SOLEC indicators (many species-based) for the Laurentian Great Lakes, it was recognized that one set of indicators was desirable so that lakes could be compared (Shear et al., 2003). To meet our similar goals, we also needed to identify a common set of species-blind

metrics across all large aquatic ecosystems to facilitate comparisons. We focused on metrics for functional groups, catch of commercially exploited fishes, changes in the catchment, and habitat alterations. We evaluated all of these metrics at the scale of the whole system. These measures allowed us to compare ecosystems on a global scale, and thereby allow a comparative assessment of the status of these ecosystems.

Building the metrics matrix for each ecosystem required a significant amount of data. All of our data were collected through numerous government and non-government programs or as part of specific research projects. For each ecosystem, we sought metric values and at least 30-year trends, plus additional ecosystem attribute data. There were numerous problems with these data including missing data, incomplete time series, limited species-related information, and limited basin coverage. Comparing these data also presented a problem as there are no consistent standardized monitoring programs for these parameters either within a region or across regions. The key to using the metrics to compare different ecosystems was to obtain comparable data which was not always possible. Unit conversion, limited data producing non-overlapping timeframes, spatial scale differences, and different human uses of the data all complicated comparisons, especially across regions. Even with these shortcomings, we believe we have captured the status of the ecosystems we examined.

The choice of trends as our entry point for analyzing the metrics was also consistent with our objective. We assume that trends are responses (including recoveries) to perturbations. Our operational definition of a healthy system within our 30-year time frame is one with few or relatively few trends. Although a trend may be positive, the existence of the trend indicates that the system was perturbed in the past 30 years. We cannot state if the system is changing toward a more or less healthy state, but we expect that in most cases the existence of trends indicates that the system is becoming more disturbed and therefore less “healthy.” Our cutoff for healthy as <50% expression of trends is meant to be conservative and recognizes the issues of data limitation and comparability and the necessarily subjective assessment required for some categories of metrics. It also recognizes that even healthy systems may express long-term trends still within a range of resilient recovery at longer time scales. The end result recognizing Superior, Tanganyika, and Baikal as the least perturbed and most healthy may not surprise the aware practitioner, but it gives us confidence in our approach because our characterization is based on an objective analysis of common metrics.

From the standpoint of ecosystem management, stable conditions are likely preferred over a trend because the outcome of a trend is undefined for the future. Multiple trends in ecosystem properties make them inherently less predictable even in the short term and potentially chaotic in the longer term if trends interact in a non-linear manner (Scheffer et al., 2001). Resilient ecosystems are systems that return to more normal states after a perturbation or stress is imposed or removed. If the return time is less than our 30-year time window, a resilient ecosystem should not show trends. It is generally agreed that resilience is a component of a healthy ecosystem (Schaeffer et al., 1988).

Ecosystem status

Based on our scale, healthy ecosystems were changing the least and thus are closer to a homeostatic state. Healthy ecosystems were large, deep lakes in relatively unpopulated areas which may help buffer them against stressors. There were no signs of eutrophication and no changes to their trophic structure over the 30-year time period. However, these ecosystems were not excluded from human impacts and experienced increases in either population or urbanization that likely account for the changes we did see. For instance, contaminants increased in Lake Baikal and nitrogen levels increased in

Lake Superior; both of these have been attributed to anthropogenic activities. Therefore, it may be more appropriate to designate these ecosystems as the “least disturbed” since they were impacted by human activities but to a much lesser extent than the other ecosystems we examined.

In ecosystems we classified as “disturbed,” the majority of metric trends were changing, indicative of multiple sources of stress. However, even in these systems, not all metrics were changing over the 30-year period. Disturbed ecosystems were, on average, shallower (Table 1) than healthy ecosystems supporting the idea that basin depth helps protect or lessen the negative influence of human activities. Increasing population pressure and urbanization impacted all of the disturbed and transitioning ecosystems and are likely responsible for the increase in fish habitat loss also occurring in these systems.

We suggest at least two important uses for this research. First, large aquatic ecosystems are complex systems and we do not completely understand how components and processes interact. We believe that the study of large aquatic systems can help guide research and management in these systems by examining the similarities and differences. For instance, there are documented regime shifts in large aquatic systems that demonstrate the impact of overfishing. One of the three regime shifts documented in the Baltic Proper, a shift from cod to sprat, was attributed to climate change and overfishing (sterblom et al., 2007). Similarly, in the Black Sea, two regime shifts have been detected, one related to a reduction of predators and the other to the expansion of an invasive species, both attributed to intense fishing pressure (Daskalov et al., 2007). Growing human populations around the world especially in developing countries (Dulvy and Allison, 2009) are increasingly reliant on fish as an important protein source with a concomitant increase in fishing pressure. Understanding the processes and signposts of regime shifts occurring in other intensely fished ecosystems may improve the likelihood of avoiding the same outcome in other systems.

Second, management and decision-making relies on forecasts of ecosystem status. This analysis was based on a 30-year time period with a focus on determining the long-term health trends as well as current ecosystem status. Significant amounts of data were examined through this process and future research will focus on the development of models to forecast changes in health status and identify possible regime shifts in large aquatic ecosystems with varying system properties. In particular, our set of aquatic ecosystems possesses remarkable ranges of ecosystem age (thousands to millions of years), biodiversity (from large endemic species flocks to glacial relict faunas), trophic state, and fishing pressure. With this method of assessing the ecosystem status of global large aquatic systems, we can now investigate how these factors interact to provide resilience or increased sensitivity to ecosystem stressors.

Acknowledgments

The post-doctoral research conducted by N. Dobiesz and the workshop were funded by the Great Lakes Fishery Commission. Additional workshop funding and support was provided by the International Joint Commission. We would like to thank all of the workshop participants and acknowledge those who do not appear in the author list including Erkki Leppkoski, Tony Pitcher, Jos Snoeks, Oliva Mkumbo, Ann Krause, Brian Shuter, John Janssen, and John Gannon. Our thanks also goes to those who contributed information to build the ecosystem matrices or reviewed the resulting matrices including Paul van Zwieten, Thomas Hrabik, Mark Ebener, David Fielder, James Johnson, Adam Cottrill, and Elena Litchman. Additionally, we would like to thank the reviewers for their thoughtful comments. This article is Contribution 1553 of the USGS Great Lakes Science Center.

Appendix A. Metrics matrix form with description of each metric, the data units preferred and the trend designations.

Units for metrics			
Metric	Description	Units	Trends
	Trends are indicated by "0" no trend, "+" increasing, "++" increase considered significant, etc.		
Trophic structure	Fish community Trophic trophic interactions		
Food chain length	Number of trophic steps from primary production to top piscivores	Number	"--,-,0,+,++"
Scale of functional groups	Number of historic functional groups (<i>see Functional Groups worksheet</i>)	List and number	n/a
Loss of functional groups	List of functional groups lost over time (<i>see Functional Groups worksheet</i>) A "+" trend indicates groups will likely continue to be lost	List and number	"--,-,0,+,++"
Within functional group diversity (at present)	For each historical functional group, list species with nominally redundant functions OR number of redundant species in each functional group (<i>see Functional Groups worksheet</i>) Trend indicates a change in the number of species by group	List or number by group or trophic level	"--,-,0,+,++"
Predator–prey balance	Mean biomass ratios between trophic level OR scale all levels on mean annual algal biomass (or biomass from chlorophyll)	Ratios by trophic level	"--,-,0,+,++"
Number of non-indigenous species	Number of successfully established non-indigenous species in each trophic level. Trend indicates trend in number of species for each trophic level	Number by level	"--,-,0,+,++"
Non-indigenous species invasion	Rate of establishment of non-indigenous species or new species over time (per decade for last century) by affected trophic level. Trend indicates status over the last century	Number or list	"--,-,0,+,++"
Exploited species	Impact of fishing		
Fisheries intrinsic stability/variability	Interannual variability in catches of exploited species (by species). Trend change in CV for each species over time.	Coefficient of variation by decade by species	"--,-,0,+,++"
Phytoplankton intrinsic stability/variability	Interannual variability in phytoplankton crop (chlorophyll a)	Annual coefficient of variation	"--,-,0,+,++"
Size range	Size range and mean size for exploited or surveyed species. Trend indicates change over time for each species	Length (cm)	"--,-,0,+,++"
Mean age at harvest	Mean age of catch (exploited species only)	Age (years)	"--,-,0,+,++"
Trends in mean age at harvest	Change per unit time in mean age (year) for exploited species, minimum 10 years of harvest	Rate	"--,-,0,+,++"
Age at maturity	Age at maturity (exploited species only) Trend indicates "+" for age increasing over time, "-" for age decreasing over time	Age (years)	"--,-,0,+,++"
Trophic structure of catch	Trends indicated by 0 no trend, + increasing, ++ increase considered significant, etc.	kg	"--,-,0,+,++"
Stocking	List of species stocked, numbers of each stocked, and trophic level. Trend indicates change in total numbers stocked by species	Number	"--,-,0,+,++"
Other species of concern	Changes in species parameters		
Species of concern	List of other species of concern	List	n/a
Size range	Size range and mean size for species or interest. Trend indicates change over time for each species	Length (cm)	"--,-,0,+,++"
Age at maturity	Age at maturity for species of interest Trend indicates "+" for age increasing over time, "-" for age decreasing over time	Age (years)	"--,-,0,+,++"
Habitat alterations	Aquatic habitat		
Nutrients (range from maximum to minimum)	Concentration range of TN, TP, and Dissolved dissolved silica from annual maximum to annual minimum. Trend indicates if range has changed over time for each nutrient	Concentration	"--,-,0,+,++"
Nutrient trends	Annual mean Concentrations concentrations of TN, TP, and dissolved Si. Trend indicates trend in annual mean for each nutrient	Concentration	"--,-,0,+,++"
Chlorophyll range (phytoplankton)	Range (max to min) of phytoplankton abundance in growing season. Trend indicates if range has changed over time	Concentration	"--,-,0,+,++"
Chlorophyll mean (phytoplankton)	Mean concentration for phytoplankton growing season for TN, TP and SI. Trend indicates trend in mean for each nutrient	Concentration	"--,-,0,+,++"
Cyanobacterial blooms	Present/absent and when change occurred; list annual trend data if available. Trend indicates whether occurrences are increasing or decreasing	Species and dates	"--,-,0,+,++"
Harmful algal species	Present/absent and when change occurred; list annual trend data if available. Trend indicates whether occurrences are increasing or decreasing	Species and dates	"--,-,0,+,++"
Transparency	Measures of visibility including Secchi depth, light extinction, turbidity. Trend indicates trend for each measure	Based on metric	"--,-,0,+,++"
Oxygen demand	Areal hypolimnetic oxygen demand (or sediment oxygen demand) Trend indicates whether area of hypoxic conditions has changed	Areal oxygen rate of depletion	"--,-,0,+,++"
Contaminants of concern	List of contaminants in species of concern for human and ecosystem health. Trend indicates whether contaminants are generally increasing or decreasing	List	"--,-,0,+,++"
Fish diseases of concern	List of fish diseases of concern by species. Trend indicates whether occurrences of fish disease are generally increasing or decreasing	List	"--,-,0,+,++"
Habitat loss	Change in habitat availability (for exploited species or species of interest) Trend indicates increasing or decreasing availability over time	List of species whose habitat has increased or decreased	"--,-,0,+,++"
Wetland/coastal nursery habitat	Change in nursery habitat availability (for exploited species or species of interest) Trend indicates increasing or decreasing availability over time	List of species whose habitat has increased or decreased	"--,-,0,+,++"
Spawning habitat	Change in spawning habitat availability (for exploited species or species of interest) Trend indicates increasing or decreasing availability over time	List of species whose habitat has increased or decreased	"--,-,0,+,++"
Catchment (watershed) change	Human impact		
Population pressure	Human population in watershed as density in land catchment AND as density per lake area. Trend indicates trend in population numbers in watershed	Numbers per area land catchment and by lake area	"--,-,0,+,++"

Appendix A (continued)

Units for metrics			
Trends are indicated by “0” no trend, “+” increasing, “+ +” increase considered significant, etc.			
Metric	Description	Units	Trends
Urbanization	Urbanization <i>Trend indicates trend of population in cities within watershed</i>	Percentage of population in cities	“ --, -, 0, +, + +”
Land use	Dominant (by area) land use in catchment (ex. protected, natural (or recovering), residential, agricultural). <i>Trend indicates trend for each land use</i>	Percentages for dominant use	“ --, -, 0, +, + +”
Economic activity	Gross domestic product of catchment populations	US dollars	“ --, -, 0, +, + +”
Ecosystem use	Ecosystem services provided by aquatic ecosystem (includes cultural or social services). A “-” trend indicates that ecosystem services have been degraded or lost.	List	“ --, -, 0, +, + +”
Other items	Miscellaneous items		
Status of benthic invertebrates	Change in abundance OR composition of benthic community. <i>Trend indicates trend in abundance</i>	Numbers or list of community changes	“ --, -, 0, +, + +”
Contaminant pathways	List of pathways through the watershed; trend represents change in number of pathways over time	List	n/a
Shoreline length	Length of shoreline in km	km	n/a

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