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Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations

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Abstract. Habitat degradation and harvest have upset the natural buffering mechanism (i.e., portfolio effects) of many large-scale multi-stock fisheries by reducing spawning stock diversity that is vital for generating population stability and resilience. The application of portfolio theory offers a means to guide management activities by quantifying the importance of multi-stock dynamics and suggesting conservation and restoration strategies to improve naturally occurring portfolio effects. Our application of portfolio theory to Lake Erie *Sander vitreus* (walleye), a large population that is supported by riverine and open-lake reef spawning stocks, has shown that portfolio effects generated by annual inter-stock larval fish production are currently suboptimal when compared to potential buffering capacity. Reduced production from riverine stocks has resulted in a single open-lake reef stock dominating larval production, and in turn, high inter-annual recruitment variability during recent years. Our analyses have shown (1) a weak average correlation between annual river and reef larval production ($\bar{\rho} = 0.24$), suggesting that a natural buffering capacity exists in the population, and (2) expanded annual production of larvae (potential recruits) from riverine stocks could stabilize the fishery by dampening inter-annual recruitment variation. Ultimately, our results demonstrate how portfolio theory can be used to quantify the importance of spawning stock diversity and guide management on ecologically relevant scales (i.e., spawning stocks) leading to greater stability and resilience of multi-stock populations and fisheries.

Key words: early life stages; ecosystem-based fisheries management; Great Lakes; Lake Erie; population demographics; *Sander vitreus*; stock discrimination; walleye.

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INTRODUCTION

Fish populations often consist of several locally distinct spawning stocks that improve population stability and resilience at larger (e.g., regional) scales through 'portfolio effects'. While portfolio theory and the concepts of diverse asset management were first developed in the financial sector (Markowitz 1952), these concepts have been applied to ecological scenarios such as fish populations (portfolios) comprised of multiple discrete spawning subpopulations (stocks; Figge 2004, Schindler et al. 2015). Portfolio effects arise in fish populations when stock-specific reproductive efforts are uncorrelated, owing to different sub-population controlling mechanisms. Reproducing at different times and locations leads to differential probabilities of success that are dependent on the environmental conditions experienced in each habitat and period (Hilborn et al. 2003). Populations that receive contributions from a diverse set of localized stocks exhibit less variability than an individual stock or a degraded population (i.e., inefficiently distributed portfolio; Markowitz 1952, Figge 2004). In turn, enhanced stock diversity should result in a population with more stable production, less risk of recruitment failure, and the ability to adapt to changing climate patterns (e.g., Hilborn et al. 2003). Therefore, portfolio theory provides a framework for the management and restoration of multi-stock population dynamics by suggesting strategies to maximize stability and resilience.

Habitat modification and harvest strategies can degrade stock diversity and reduce the natural benefits of evolved portfolio effects. Individual stocks may decline in abundance, be extirpated, or change spawning habitat types when suitable habitat is lost (Koonce et al. 1996, Moore et al. 2010, Carlson and Satterthwaite 2011). Additionally, aggregate management can result in disproportionate harvest and extirpation of some component stocks, reducing diversity, especially in large-scale fisheries with complex stock structures (Stephenson 1999, Smedbol and Stephenson 2001, Hutchinson 2008). Habitat loss and harvest result in homogenization of life history characteristics, reduction in spatial stock complexity, and temporally synchronized spawning events (Smedbol and Stephenson 2001, Moore et al. 2010, Schindler et al. 2010). Failure to recognize and maintain stock diversity through management can lead to the degradation of portfolio effects and limit naturally evolved buffering capacities, and resilience to environmental change.

Multi-stock management concerns and the recognition of portfolio effects have focused mainly on large-scale marine and anadromous fish populations (e.g., Hilborn et al. 2003, Moore et al. 2010, Schindler et al. 2010); however, analogous situations occur in large freshwater systems (e.g., Laurentian Great Lakes). Freshwater systems offer a diversity of habitat types for reproduction. For example, a number of fish populations (e.g., *Osmerus mordax* rainbow smelt, walleye, and *Morone chrysops* white bass) are comprised of both riverine- and lake-spawning stocks and are therefore likely to exhibit strong portfolio effects. Spawning areas within rivers can be highly segregated from the main lake, creating the possibility that eggs and larvae experience distinct environmental conditions. Further, anthropogenic disturbances (i.e., dredging, damming, shoreline hardening and watershed alterations) often negatively affect the coasts of large freshwater ecosystems; leading to habitat degradation and sometimes high fishing pressure where spawning occurs (Mapes et al. 2014). Therefore, the application of portfolio theory in complex freshwater ecosystems could provide a tool for managing harvested or sensitive populations and support efforts for biodiversity conservation (Abell 2002).

Applying portfolio theory to fisheries management decisions can provide valuable insights into the interaction of component stocks and could inform targeted restoration or protection of sensitive stocks; potentially facilitating an adaptive management approach (Williams 2011). The application of portfolio theory requires stock specific data such as spawning stock abundance (Begg and Marteinsdottir 2002, Carlson and Satterthwaite 2011), larval production (herein), or juvenile abundance (Marteinsdottir et al. 2000*a*, *b*). These metrics are analogous to those used in the financial sector such as investment (spawning stock abundance), price or return (larval or juvenile abundance), and value (often referenced as return-on-investment or ROI), used here as the expected return given some level of investment. Although these types of information are routinely collected as a part of fish stock assessments, portfolio theory has not been used to evaluate specific fisheries management strategies or suggest alternative management options.

Herein, we seek to use portfolio theory to suggest management options for a multi-stock freshwater fish population that is currently subject to spawning habitat degradation, experiences substantial fishing pressure, and exhibits wide fluctuations in recruitment. Our specific objectives were to: (1) assess spatial and temporal diversity in larval production, (2) quantify the current degree of buffering and potential buffering capacity in larval production, and (3) suggest management options to forward the maintenance and improvement of the larval production portfolio to enhance population resiliency and reduce the risk of fluctuations in population numbers.

We used Lake Erie walleye as a case study to show how portfolio theory can guide conservation and restoration efforts of multi-stock fish populations. We focused on the larval stage in this assessment for several reasons. First, recruitment variation of most ecologically and economically important fish populations, including walleye (Mion et al. 1998, Roseman 2000, Ludsin et al. 2014), appears to be regulated by early life growth and survival. Second, the physical (e.g., wind-driven water circulation, upwelling; Hjort 1914, Lasker 1981, Iles and Sinclair 1982) and biological (e.g., prey availability, predation; Hjort 1914, Cushing 1990, Carreon-Martinez et al. 2014) processes that control early life growth and survival oftentimes are heterogeneous in both space and time (Houde 2008, 2009, Ludsin et al. 2014). In turn, the progeny of spawning stocks that are spatially and (or) temporally segregated would be expected to be strongly regulated by different (localized) processes, resulting in uncorrelated (i.e., asynchronous) recruitment. This differs from older life stages (e.g., juvenile, adult) during which time individuals are less susceptible to regulation by localized environmental conditions (Houde 1987, Ludsin et al. 2014) and they tend to experience similar regulatory controls by migrating into similar habitats where they form a mixed-stock population (Iles and Sinclair 1982, Wang et al. 2007). These considerations indicate that portfolio effects should be stronger during early life stages than later ones.

METHODS

System description

Lake Erie walleye is a multi-stock population that utilizes geographically distinct spawning habitats. Adult walleye migrate throughout the lake and into Lake Huron during summer and fall, but exhibit spawning site fidelity when returning to the four major spring spawning habitats including; Maumee, Sandusky and Detroit Rivers, and an open lake reef complex (Wang et al. 2007; Fig. 1). Each spawning habitat exhibits unique characteristics resulting in different physical responses to regional environmental conditions that may influence larval production and survival. For example, the Maumee and Sandusky rivers flow through watersheds dominated by agricultural land use with low gradients and are subsequently highly responsive to regional temperature fluctuations and extreme precipitation events (Richards 1990; Pritt et al., *unpublished manuscript*). High variability in temperature and flow regimes in these systems can influence timing of production and larval survival (Mion et al. 1998, Crane and Farrell 2013, Pritt et al. 2013, DuFour et al. 2014). The open-lake reef complex is located in relatively shallow water influenced by Maumee and Detroit River discharge, and is responsive to regional temperature fluctuations. The reefs are influenced by strong wind events that can disrupt spawning and incubation and cause undesirable transport of eggs and hatched larval fish (Roseman et al. 2001, Zhao et al. 2009, Humphrey et al. 2012). Finally, the Detroit River, a natural channel connecting lakes Erie and Huron, represents a very stable spawning habitat (Pritt et al., *unpublished manuscript*) as it is unaffected by wind and precipitation events (Holtschlag and Koschik 2001). Larval fish from each local spawning area are exported to the open lake, and transported in discrete water masses during the earliest stages of growth (Fraker et al. 2015). The spatial and temporal isolation experienced during the early life stages are thought to result in genetically distinct spawning stocks from each area (Merker and

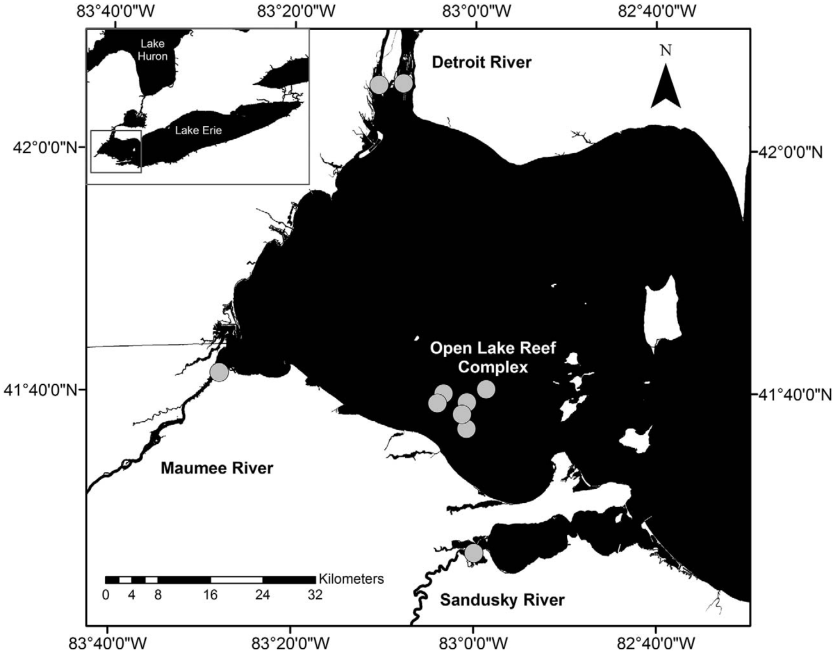

Fig. 1. Lake Erie's western basin showing sampling locations used to determine stock-specific larval production (gray circles), including the Maumee, Sandusky, and Detroit Rivers, as well as the open-lake reef complex.

Woodruff 1996, Strange and Stepien 2007).

The population structure and spawning habitat characteristics of walleye suggest that portfolio effects might stabilize population dynamics, but anthropogenic forces have adversely affected these stocks and habitats, particularly the riverine stocks. For example, the Maumee and Sandusky River watersheds were once dominated by swamp forests, including the great "Black Swamp" (Kaatz 1955). They were drained and deforested during the late 1800s, however, and are now predominantly used for agriculture. These changes have resulted in highly variable and extreme discharge events and increased sediment loads (Karr et al. 1985, Richards 1990, Richards et al. 2008). In addition, both river systems have barriers to fish movement. Initially built in the 1840s at rkm 55, the Providence and Grand Rapids dams restrict upstream access on the Maumee River (Zheng et al. 2009), whereas the Ballville Dam, built in 1911 at rkm 29, restricts access to upstream spawning grounds on the Sandusky River (Cheng et al. 2006, Gillenwater et al. 2006). In the Detroit River, dredging and re-deposition of riverbed material, to support shipping channel construction and maintenance, has resulted in spawning and nearshore nursery habitats losses, as well as changes in flow dynamics (Bennion and Manny 2011, Hondorp et al. 2014). Although stock-specific records of abundance declines do not exist for any of these subpopulations, it is widely accepted that habitat degradation has negatively affected their individual contributions to lake-wide production (Reiger et al. 1969, Hartman 1973, Reiger and Hartman 1973, Trautman and Gartman 1974, Karr et al. 1985, Koonce et al. 1996).

Additionally, walleye support prized sport and commercial fisheries where individual stocks are managed collectively as a single population through a binational agreement (Hatch et al. 1987, Locke et al. 2005, Roseman et al. 2012*a*) across five jurisdictions (Michigan, Ohio, Pennsylvania, New York, USA and Ontario, Canada). Disproportionate harvest also may contribute to a disruption of portfolio effects by reducing the abundance of riverine stocks (Koonce et al. 1996, Stephenson 1999). During the past 30 years, Lake Erie walleye recruitment to this population has varied greatly (i.e., >1,000 fold; WTG 2014), often causing the entire fishery to be supported by dominant year-classes (Vandergoot et al. 2010). In response to concerns about sources of recruitment variation, larval walleye production has been quantified periodically from each of the four major spawning systems in Lake Erie.

Larval fish sampling in rivers

We collected larval walleye using ichthyoplankton net tows conducted downstream of three major spawning areas in Lake Erie's western basin, including the Sandusky River during an early (1994–1995) and late (2011–2013) period, Maumee River during an early (1994–1995) and late (2010–2014) period, and Detroit River during a mid (2006–2007) and late (2010–2014) period (Fig. 1). Specific sampling protocols and spatiotemporal sampling intensity varied among spawning areas (Table 1). Briefly, samples were collected from the Maumee and Sandusky rivers three times per week during late-March through May in the early period with a neuston net (500 μm mesh; Mion et al. 1998). During the late period, the Maumee River was sampled three times per week during late March through early June with paired bongo nets (333 and 500 μm mesh; DuFour et al. 2014). Late period Sandusky River sampling followed methods described above for early period sampling by Mion et al. (1998) using conical and paired bongo ichthyoplankton nets once per week. We collected Detroit River samples with bongo nets (333 and 500 μm) from major channels emptying into Lake Erie once per week during mid-April through early June (Roseman et al. 2012*b*). All ichthyoplankton tows included flowmeters to estimate volume of water sampled, and facilitated density calculations. Larvae were preserved in ethanol until laboratory identification using myomere counts (Auer 1982), and enumeration. In each larval collection area, sampling generated larval walleye densities measurements ($L\_D_{ijk} = \text{larvae/m}^3$) for each individual net (i) on each sampled day (j) and year (k), spanning the larval walleye drift season (March through early June).

Egg sampling on reefs

Collecting known reef larvae is difficult because water currents transport fish immediately upon hatching, resulting in wide distribution and overlap among stocks (Fraker et al. 2015). However, walleye eggs adhere to bottom substrates and presence signifies spawning location; therefore, we used a different strategy to measure reef production. We collected eggs from six major spawning reefs: Niagara, Toussaint, Round, Crib, Cone, and Locust during the late (2011–2014) period (Fig. 1). In the early period (1994–1995), we used data from Roseman et al. (1996) where eggs were collected from only the dominant Niagara and Toussaint reefs. Walleye egg sampling began in late March during all years (after ice-out) and continued once per week until early May when spawning ceased and catches of walleye eggs were negligible. Methods for the early period sampling are outlined in Roseman et al. (1996), but briefly discussed here. An egg pump, comprised of a 39 kg iron sled (0.25 m wide; Stauffer 1981) attached to a diaphragm pump at the surface by a flexible hose 5 cm in diameter, sucked eggs off the reef surface. We towed the sled nine times per site per sampling date for 2 min at ~0.5 m/s. During 2011–2013, we used furnace filters, also referred to as egg mats, a common substrate used for the collection of eggs (Nichols et al. 2003, Manny et al. 2007, Ivan et al. 2010). During 2011, we wrapped furnace filter around cement blocks then chained three wrapped blocks together to create a gang. We positioned one gang per reef. During 2012 and 2013, we placed furnace filters into custom designed aluminum frames, 61 × 91.5 cm, which sat flat on the lake bottom and were weighed down by 32 kg of cement. We positioned one frame at each reef and replaced the furnace filter each week. Once eggs were separated from debris (early period) or removed from the furnace filter (late period), identification was based on size, color, and viability. Eggs that showed signs of opaqueness or exhibited fungal growth were categorized as dead (Roseman et al. 1996). We enumerated and averaged live walleye eggs by site and day to obtain a single density per 2 min tow (early period) or a single number per m^2 (late period).

A comparison study was performed in 2014 to account for differences in sampling methods, where we sampled multiple reefs simultaneously with egg mats and the egg pump during the walleye spawning season. Density observations from each sampling method were highly

Table 1. Summary of sampling efforts in four western Lake Erie larval walleye production areas; included are the years sampled, the number of samples collected in each year (N), the gear used, and the start and end dates of sampling.

System	Year	N	Net type	Mesh sizes (μm)	Start date	End date
Maumee	1995	50	Neuston	500	28 Mar	31 May
Maumee	1994	44	Neuston	500	31 Mar	31 May
Maumee	2010	179	Paired bongo	333 and 500	13 Apr	1 Jun
Maumee	2011	144	Paired bongo	333 and 500	26 Apr	1 Jun
Maumee	2012	183	Paired bongo	333 and 500	22 Mar	29 May
Maumee	2013	166	Paired bongo	500	26 Mar	30 May
Maumee	2014	201	Paired bongo	500	8 Apr	2 Jun
Sandusky	1994	48	Neuston	500	29 Mar	31 May
Sandusky	1995	44	Neuston	500	30 Mar	31 May
Sandusky	2011	32	Conical	500	30 Apr	19 May
Sandusky	2012	42	Paired bongo	500	4 Apr	26 Apr
Sandusky	2013	24	Paired bongo	500	23 Apr	23 May
Sandusky	2014	5	Neuston	500	25 Apr	20 May
Detroit	2006	128	Paired bongo	333 and 500	18 Apr	1 Jun
Detroit	2007	68	Paired bongo	333 and 500	20 Apr	5 Jun
Detroit	2010	96	Paired bongo	500	15 Apr	2 Jun
Detroit	2011	102	Paired bongo	500	13 Apr	3 Jun
Detroit	2012	210	Paired bongo	500	13 Apr	4 Jun
Detroit	2013	188	Paired bongo	500	17 Apr	3 Jun
Detroit	2014	190	Paired bongo	500	15 Apr	3 Jun
Reefs	1994	11	Egg pump	500	1 Apr	17 May
Reefs	1995	22	Egg pump	500	1 Apr	17 May
Reefs	2011	28	Egg mat	...	6 Apr	3 May
Reefs	2012	42	Egg mat	...	20 Mar	2 May
Reefs	2013	34	Egg mat	...	3 Apr	8 May
Reefs	2014	21	Egg mat	...	18 Apr	8 May

Note: Egg mat samples were not filtered through mesh netting.

skewed, thus we normalized the paired data using a multivariate Box-Cox transformation (Box and Cox 1964), to ensure that data conformed to a bivariate normal distribution. After transformation, egg densities from the egg mats were strongly correlated ($n = 17$; $\rho = 0.73$) with abundances observed with the egg pump. We then used the bivariate normal distribution conditional formula to convert egg pump (number of eggs/2 min tow) collected in 1994 and 1995 to egg mat densities (number of eggs/m^2) based on the relationship established through the 2014 comparison study. Conversions allowed for direct comparison of estimated (1994 and 1995) and observed egg mat densities (2011–2013), and subsequent extrapolation to larval production (May 2015). From the reefs, sampling and conversions generated walleye egg densities measurements ($E\_D_{ijk} = \text{eggs/m}^2$) for each sampling event (i) during each week (j) and year (k), spanning the walleye spawning season (late March through early May).

Larval fish abundance estimation from rivers and reefs

For each river system, larval density measurements (L_D_{ijk}) were used to estimate daily and annual larval production. Prior to abundance estimation, we subset observed larval density time-series to the active drift seasons by including one zero observation day before and after the earliest and latest observed larval walleye collected within each larval production area. The active drift period for each area was different, and therefore the estimated periods differed. We used a modification of the Bayesian state-space model described in DuFour et al. (2014) to estimate production from each area. Modifications included a reparameterization of the state process to share information directly through the mean (λ_{jk}) and precision (τ_{jk}) of the upper level gamma distribution, rather than through shape (α) and scale (β) parameters. In addition, we modeled all years simultaneously and shared precision information from the time varying precision parameters across years through a global hyper-prior (τ_{global}). These changes aided in model convergence, and allowed for the direct estimation of mean densities rather than calculation as a latent variable (Eq. 1).

$$\begin{aligned} &\tau_{global} \sim \text{gamma}(1, 1) \\ &\tau_{jk} \sim \text{gamma}(\tau_{j-1k} \times \tau_{global}, \tau_{global}) \\ &\lambda_{jk} \sim \text{gamma}(\lambda_{j-1k} \times \tau_{jk}, \tau_{jk}) \\ &L\_D_{ijk} \sim \text{Poisson}(\lambda_{jk}) \end{aligned} \qquad (1)$$

We expanded estimated daily densities (λ_{jk}) to abundance by multiplying by average daily river discharge within each year and reported mean values. We estimated annual production by summing daily abundance estimates within years and reported the most probable values (i.e., distribution peak) and 50% and 95% highest density intervals (Kruschke 2010). We calculated mean daily abundance by averaging daily abundance across years and reported mean values.

For the open-lake reef complex, egg density measurements (E_D_{ijk}) were used to estimate weekly and annual larval production. Although not all reefs were sampled during all years, we considered individual reef measurements as random samples from the entire reef complex, and therefore pooled weekly egg density measurements. Doing so allowed us to estimate egg densities and production for the entire reef complex across years with minimal additional assumptions. Similar to the larval data in other production areas, we subset observed egg density time series to an active spawning season, by including one zero observation week before and after the earliest and latest observed walleye eggs collected across years. We used the same model described above to estimate weekly and annual egg production, with j representing week rather than day. We expanded estimated weekly densities (λ_{jk}) to abundance by multiplying by total reef area as calculated by Bolsenga and Herdendorf (1993). We estimated weekly larval production by multiplying weekly egg production by a mortality rate of 99.5%, the reported mortality rate of walleye from egg to 10 mm total length (Forney 1976). We considered the inverse, survival rate, as a random variable and added this calculation to the egg production model. We described survival with a beta distribution (beta(5, 1000)), with mean of 0.005% and standard deviation of 0.002% allowing survival to nearly span 0–0.01% or 99–100% mortality. We report the mean values of weekly larval production. Annual larval production was calculated by summing weekly larval production within years, and we and reported most probable values as well as the 50% and 95% highest density intervals.

To compare the timing of larval fish hatching between the open-lake reef complex and larval export from the rivers, we calculated weekly hatch dates for eggs captured on the egg mats using a temperature-dependent egg development equation (Jones et al. 2003) and daily water temperature data provided by the City of Toledo Collins Park Water Treatment Plant. The water intake is located approximately 16 km west of the open-lake reef complex. For each week that we estimated egg densities, we used a median date between our weekly samples to act as a "start date" for hatch-date calculations. We estimated average larval hatch patterns by taking the average production associated with each weekly egg density estimate and the average Julian day from extrapolated hatch dates across years.

The Bayesian state-space models used here share spatial-temporal information that helps account for patchiness in the larval drift and egg deposition, informs estimates of unsampled days and weeks, and improves accuracy and precision of annual abundance estimates. We ran separate models for each system (four total) using the Markov chain Monte Carlo (MCMC) based software, OpenBUGS v3.2.2 (Lunn et al. 2009). OpenBUGS was activated and results were summarized through the R2OpenBUGS v3.2-2.2 package (Sturtz et al. 2005) within the R software environment (R Core Team 2013). Each model used three mixing chains including 2,000 iterations and a 500-iteration burn-in period per chain. Posterior samples were thinned so that 1 of every 10 iterations was used in subsequent analysis. Convergence was assessed through visual monitoring of chain history and the R-hat statistic (Gelman and Hill 2007, Gelman et al. 2014).

Portfolio analysis

Larval fish production estimates spanned nine years (1994, 1995, 2006, 2007, and 2010–2014) and four independent larval production areas. However, congruent sampling of all systems occurred only during four consecutive years

(2011–2014). To take greater advantage of the time series, while maintaining the integrity of correlations between systems, we first omitted years 2006 and 2007 from the portfolio analysis. In addition, we substituted system-specific mean production for missing estimates from unsampled years during 1994, 1995 and 2010. Substitutions included one year (2010; mean = 2.00) for the Sandusky River, two years (1994 and 1995; mean = 49.80) for the Detroit River, and one year (2010; mean = 1,087.08) for the open-lake reef complex. Substituting mean production estimates for missing values maintained realistic fluctuation magnitudes within stocks and had only a minor effect on correlation estimates used in the portfolio analysis (M. R. DuFour, *unpublished data*).

Portfolio effects depend on stock prices, returns, variation and correlation in returns, investments, and relative stock values. In this analysis, we only measured returns (larval production) from an unknown investment; therefore, the relative value (return on investment; ROI) of each spawning stock is unknown. Lacking investment information (stock-specific spawner abundance), we assumed that mean returns (larval production) are proportional to investment (spawning stock size) and therefore the average ROI from each spawning stock is equal. Further, we assumed that the magnitude of larval production was indicative of a stock's price, or the realized value of a stock based on the current "market conditions" (i.e., environmental conditions). We used the most probable values from annual production estimates (P_i), and calculated the relative return (R_i; Eq. 2) as production gain or loss across the period of interest (Elton and Gruber 1987).

$$R_i = \frac{P_i - P_{i-1}}{P_{i-1}} \qquad (2)$$

We assessed portfolio performance using methods developed by Markowitz (1952), and calculated expected portfolio return and variance. Expected return ($E(R_p)$; Eq. 3) is the sum of mean relative returns from an individual stock (μ_i) and their proportional contribution (x_i) to the portfolio. Expected variance ($V(R_p)$; Eq. 4) is calculated with the variance (σ_i^2), standard deviation (σ_i), and proportional contribution (x_i) of individual stocks. In addition, portfolio variance accounts for the correlation between individual stocks over time, calculated as Pearson's correlation coefficient (ρ_{ij}). In short, a portfolio with a given expected return is preferred over an alternative portfolio with a similar return but larger expected variance. In the latter scenario, a manager would be accepting additional risk for the same benefit.

$$E(R_p) = \sum x_i \mu_i \qquad (3)$$

$$V(R_p) = \sum x_i^2 \sigma_i^2 + 2 x_i x_j \sigma_i \sigma_j \rho_{ij} \qquad (4)$$

Financial researchers have modified Markowitz' work with the intent of improving estimated means and variances, as well as expected correlation coefficients (Elton and Gruber 1973). In particular, the assumption of correlation structure can affect quality of portfolio assessment and accuracy of predicted performance. Here, we used the "constant correlation model," ("mean model" sensu Elton and Gruber 1973), which makes a simplifying assumption about the correlations between individual stock returns (R_i). This model asserts that observed pairwise correlations between stocks are random samples from true correlations. The true correlation between stocks is naively assumed to be zero (i.e., no relationship between individual systems), whereas the true correlation estimate is taken as the mean of individual pairwise stock correlations (Eq. 5). The constant correlation estimate was substituted into the calculation of portfolio variance (Eq. 4). Although this may seem like an unrealistic simplification, tests of the "constant correlation model" consistently outperformed predictive accuracy of more complex correlation structures, including the use of observed correlations (Elton and Gruber 1973, Elton and Gruber 1987). In our situation, we have a short time-series with only a few stocks, which precludes the use of more complex correlation structures and provides a small sample of observed correlations. Therefore, the "constant correlation model" is a conservative choice for evaluating portfolio performance and developing alternative management options.

$$\overline{\rho} = \frac{\sum \rho_{ij}}{n} \qquad (5)$$

Using observed data and the tools describe above, we developed a set of hypothetical portfolios by manipulating the proportional contribution (x_i) from each stock. Each combination of stocks had a unique expected risk and return. We plotted risk on the x-axis and return on the y-axis allowing visual comparison of the cloud of potential portfolios. As stated before, portfolios with the same expected return (y-value) but smaller expected risks (further left on the x-axis) are preferred. The "efficient frontier" bounded the cloud of portfolio options to the left, and represented the lowest risk possible for a given expected return. Depending on a manager's risk tolerance, it is advisable to invest somewhere along the efficient frontier. Although many investment options exist on the efficient frontier, only one optimizes risk and return based on the risk free rate (R_f) and Sharpe ratio. The risk free rate theoretically represents the expected return from a risk-free investment. In our scenario (larval fish production), it would be difficult to imagine a situation with negligible risk, except maybe in controlled hatchery settings. Therefore, in this study we set R_f equal to zero. The Sharpe ratio is a measure of the portfolio efficiency, and is calculated as the expected return less the risk free rate, divided by the expected risk (Eq. 6, Sharpe 1966). With the risk-free rate set, we can calculate the "capital market line" and identify the optimal portfolio (i.e., market portfolio). The capital market line intersects the y-axis at the R_f, and is tangent to the efficient frontier at the point with the highest Sharpe ratio. The line is defined by an intercept at R_f and slope of the intersected portfolio's Sharpe ratio on the efficient frontier (Elton and Gruber 1987).

$$\text{Sharpe ratio} = \frac{R_p - R_f}{\sigma_p} \qquad (6)$$

We used the R package 'stockPorfolio' (Diez and Christou 2012) to perform an analysis based on the methods described above and developed management options to improve efficiency of larval walleye production in Lake Erie. We simulated 3,000 potential portfolios and exported the proportional investment, and expected risk and return for each. We identified the efficient frontier (left boundary of potential portfolios) and highlighted the section that could realistically be achieved through management actions. This excludes portfolios achieved through "short selling," or negative contributions, which from an ecological standpoint is unreasonable. Within this realistic section of the efficient frontier, we compared the proportional contribution, expected risk, and expected return between our current portfolio and five targeted management options. The five targeted management options included: (1) optimize return while maintaining the current risk level, (2) optimize risk while maintaining the current return rate, (3) optimize risk and return based on the risk free return rate (R_f) and Sharpe ratio, and (4–5) provide two intermediate options for use in an adaptive management approach (Williams 2011). Further, we calculated the system-specific changes in larval production necessary to achieve each management option to evaluate feasibility and inform an adaptive approach.

RESULTS

Spatial and temporal diversity in larval abundance

The majority of larval production across systems and years occurred during early to mid-May (Fig. 2). However, some systems showed a greater diversity in temporal production than others. The Maumee River showed the greatest temporal range of production with hatching events spanning 73 d (22 March–2 June) across sample years (1994, 1995, 2010–2014). The open-lake reef complex also had a wide temporal range of hatching events spanning 61 d (2 April–1 June) across sampling years (1994, 1995, 2011–2014). The Sandusky and Detroit rivers exhibited shorter temporal hatching windows with the Sandusky spanning 55 d (3 April–27 May) across sampling years (1994, 1995, 2011–2013) and the Detroit spanning 54 d (13 April–5 June) across 2006, 2007, and 2010–2014. The number of significant hatching events, defined as peak events greater than a system's daily average across years, was greater in the Maumee and Sandusky rivers than the Detroit River or open-lake reef complex. Peak hatching events also varied in time. Consistency in peak hatching events was greatest in the Detroit River and open-lake reef complex as both systems produced fewer peak events per year with these events temporally clustered across years. Each system experienced early hatching during 2012,

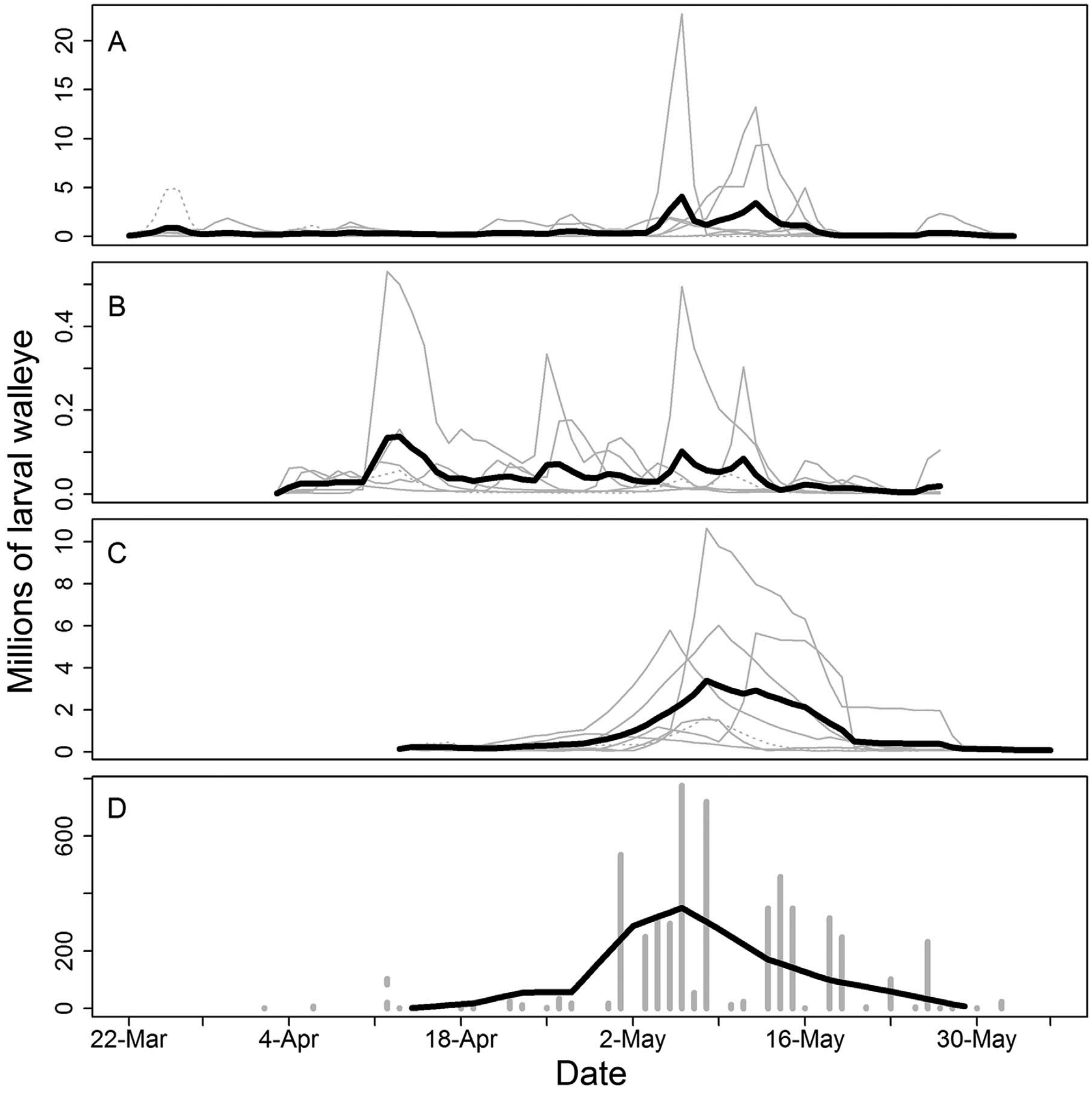

Fig. 2. Summary of larval walleye production estimates across years (1994, 1995, 2010–2014) for the (A) Maumee, (B) Sandusky, and (C) Detroit rivers and (D) western Lake Erie's open-lake reef complex. Thin gray lines represent the daily mean production estimates for each year for rivers, whereas gray bars represent weekly mean production estimates for reefs. The black line represents the average daily and weekly production estimates for each larval production area. The dashed gray lines and bars highlight the response of peak hatching in each system to unseasonably warm temperatures during 2012.

which had an unusually warm spring, with peak events shifting toward the early part of the hatching season (Fig. 2). The greatest temporal shifts in peak events were in the Maumee and open-lake reef complex, followed by the Sandusky and Detroit rivers.

Total annual production (most probable values, P_i) of larval walleye from each system varied across sampled years (Table 2, Fig. 3). Open-lake reef contributions dominated all other production areas in each year with the most probable values of larval production from this area

Table 2. Most probable values of annual larval walleye production in four western Lake Erie spawning stocks and associated summary statistics.

	Annual production, P_i (millions of larvae)							Summary statistics		
Stock	1994	1995	2010	2011	2012	2013	2014	SD	Mean	CV
Maumee	22.75	49.20	70.00	50.00	18.80	57.00	9.25	22.60	39.57	0.57
Sandusky	2.90	1.45	2.00	1.75	0.72	3.70	1.50	1.00	2.00	0.50
Detroit	49.80	49.80	15.85	55.00	17.00	12.25	117.00	36.60	45.24	0.81
Reef	2200.00	1700.00	1087.08	300.00	172.50	750.00	1400.00	739.57	1087.08	0.68

ranging from 172.50 million to 2.20 billion. The second greatest producers were the Detroit and Maumee rivers with their most probable values ranging between 12.25–117.00 and 9.25–70.00 million, respectively. The Sandusky River contributed a minimal amount of larvae in all years with its most probable values ranging between 0.72 and 3.70 million. Estimated production from each system appeared to vary normally across years around the mean; however, the magnitude of variation increased with mean (Table 2). Relative variation, denoted by the coefficient of variation (CV), was greatest in the Detroit River, followed by the open-lake reef complex, and then the Maumee and Sandusky rivers. Uncertainty around annual estimates varied depending on the temporal and spatial sampling coverage and variability within the data. However, the order of magnitude differences between most systems and minimal overlap of credible intervals among systems with similar magnitudes (i.e., Maumee and Detroit) allowed for reasonable correlation estimates.

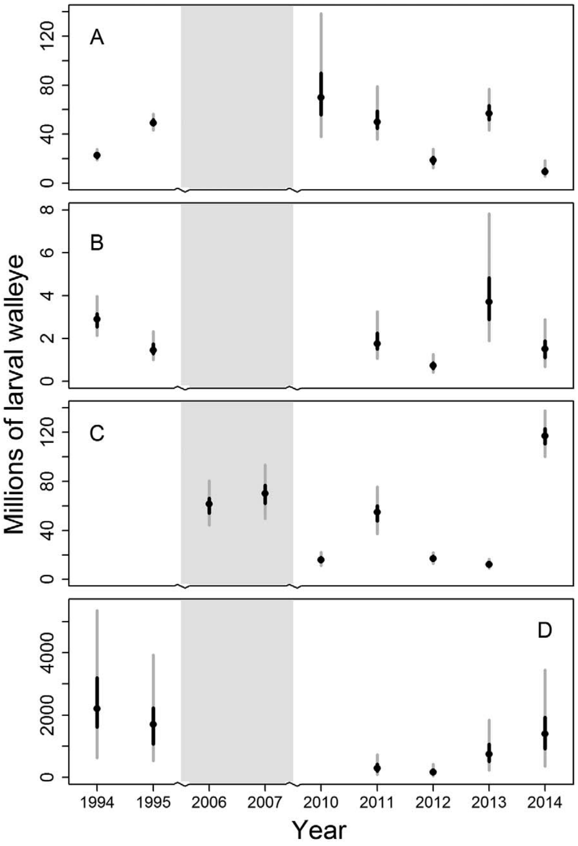

Fig. 3. Annual larval walleye production estimates for the (A) Maumee River, (B) Sandusky River, (C) Detroit River, and (D) western Lake Erie's open-lake reef complex. Black dots represent the most probable values (P_i), whereas black and gray lines respectively represent 50% and 95% highest density intervals. We omitted values in the gray region from the portfolio analysis. Note that the y-axis differs among panels.

Portfolio analysis

Relative returns (R_i) from individual stocks followed a similar pattern as the CV of the most probable larval production estimates (Table 3). The Detroit River had the highest mean returns but also the greatest fluctuation around the mean, followed by the open-lake reef complex, and then the Maumee and Sandusky Rivers. Correlation between individual stocks fluctuated around zero (Table 4). The strongest relationships were between the Maumee River, Sandusky River, and open-lake reef complex (ρ_{ij} ranged between 0.62 and 0.88). Negative correlations were observed between the Detroit and Maumee Rivers ($\rho_{ij} = -0.55$) and the Detroit and Sandusky rivers ($\rho_{ij} = -0.32$). Correlation between the Detroit River and open lake reef complex was close to zero ($\rho_{ij} = 0.05$). The constant correlation estimate, average of individual correlations, was weakly positive ($\overline{\rho} = 0.24$) and not strongly influenced by the substitution of mean produc-

Table 3. Relative returns from individual spawning stocks and associated summary statistics.

Stock	Relative returns, R_i							Summary statistics	
	1994	1995	2010	2011	2012	2013	2014	SD	Mean
Maumee	. . .	1.16	0.42	−0.29	−0.62	2.03	−0.84	1.12	0.31
Sandusky	. . .	−0.50	0.38	−0.13	−0.59	4.12	−0.59	1.84	0.45
Detroit	. . .	0.00	−0.68	2.47	−0.69	−0.28	8.55	3.62	1.56
Reef	. . .	−0.23	−0.36	−0.72	−0.43	3.35	0.87	1.54	0.41

Note: The relative returns for 1994 cannot be calculated without 1993 estimates.

tion estimates for unsampled years ($\overline{\rho}$ change of 0.18–0.24).

The current portfolio (Fig. 4, black square: C) is not efficient, i.e., it was not part of the ecologically realistic section of the efficient frontier (thick black line). All management options included increases in the production from riverine stocks and improvements in the return to risk ratio (i.e., Sharpe ratio; Table 5). Management option one (1 Opt Return, Table 5; black circle: 1, Fig. 4) simulated optimizing the expected return from the portfolio while maintaining the current risk. This could be achieved with substantial increases in percent contribution from river stocks, with the Maumee and Detroit each contributing proportionally more (32 and 30%, respectively) than the open-lake reef complex (23%), and the Sandusky (15%). From a manager's perspective, predictability of total larval production would not change but on average, more fish would be produced. Management option two (2 Opt Risk, Table 5; black circle: 2, Fig. 4) simulated optimizing the risk while maintaining the current return, with contributions dominated by the Maumee (53%) and open-lake reef complex (25%). With this option, the Sandusky (14%) and Detroit (8%) rivers contributions would be increased over current production, but still proportionally much less than Maumee and reef stocks. In this scenario, we assume that production from the currently dominant reef stock will not decline, but that river stock production can be increased. From a manager's perspective, this scenario would result in production similar to the return optimization, but with a greater capacity to predict year-to-year production. Management option three (3 Opt Port, Table 5; black circle: 3, Fig. 4) simulated optimizing both risk and return and resulted in recommended contributions of, 35% Maumee, 15% Sandusky, 27% Detroit, and 23% open-lake reef complex. This option would provide the most efficient larval production scenario as indicated by the highest Sharpe ratio (0.4944, Table 5). From a management perspective, this scenario provides the most predictable production (lowest risk) at the largest magnitude (highest return) possible. Management option four (4 Inter-1, Table 5; black diamond: 4, Fig. 4) simulated incremental improvements in risk and return through minor changes from the current portfolio with 4% Maumee, 3% Sandusky, 7% Detroit, and 86% open-lake reef complex contributions. This option provides an intermediate management goal for use in an adaptive approach. If the benefits of achieving this goal outweigh the cost, managers may choose to set an additional intermediate goal for future evaluation in progress towards a fully optimized production portfolio. Management option 5 (5 Inter-2, Table 5; black diamond: 5, Fig. 4), provides a second intermediate management goal, increasing proportional contributions to 10% Maumee, 7% Sandusky, 18% Detroit, and 66% open-lake reef complex.

All management options described above (also see Table 6) indicated that increased production from rivers would promote population-level production stability, with production from each riverine stock exceeding that of the open-lake reef complex in the most efficient management options (Options 1–3; Table 6). The relative

Table 4. Pearson's correlation coefficient (ρ_{ij}) between relative returns from individual larval walleye production areas and constant correlation estimate.

Stock	Maumee	Sandusky	Detroit
Maumee	1	. . .	. . .
Sandusky	0.78	1	. . .
Detroit	−0.55	-0.32	1
Reef	0.62	0.88	0.05

Note: Missing values represent duplicates.

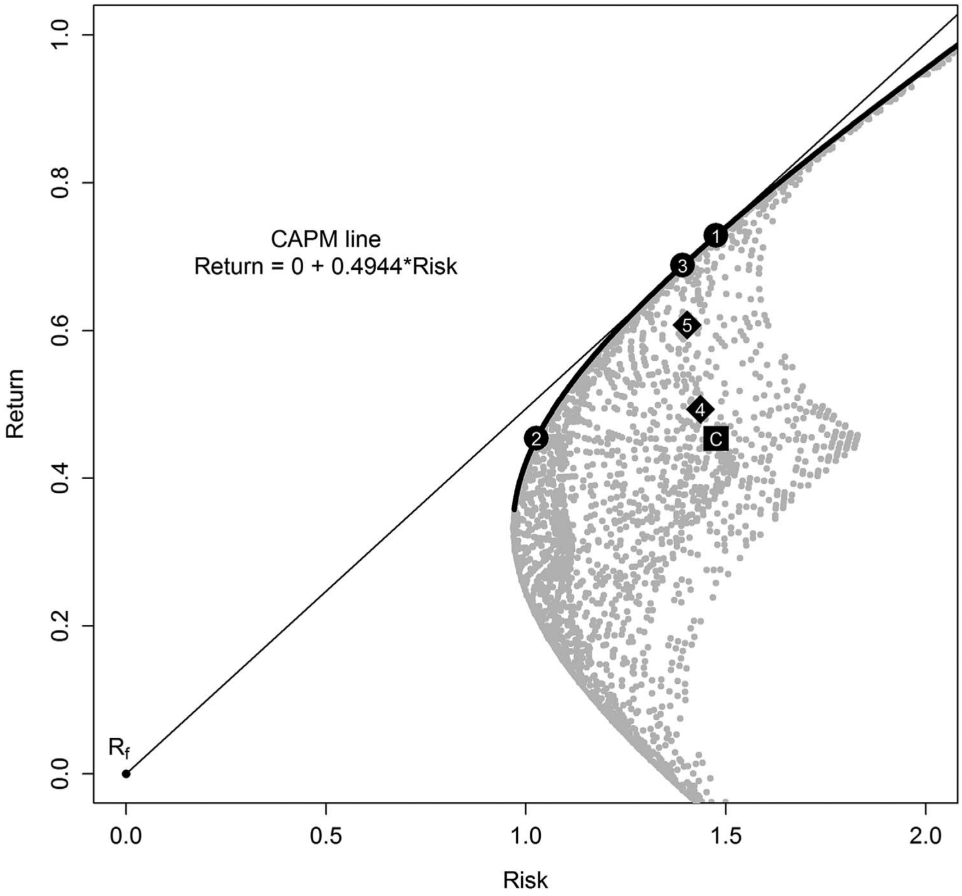

Fig. 4. Visual depiction of portfolio analysis include cloud of potential portfolios (gray dots), current larval production portfolio (black square , C), realistic section of the efficient frontier (thick black line), five management portfolio options (black circles 1–3; black diamonds 4–5), risk free investment rate (small black dot, R_f), and capital market line (thin black line).

increases ranged from 33-59 fold in the Maumee, 312-346 fold in the Sandusky, and 8 to 31 fold in the Detroit River for portfolios lying on the efficient frontier (Options 1–3). Intermediate management options (Options 4–5) did not require as great a magnitude of production increase form riverine stocks but still showed improvement in portfolio efficiency, with Sharpe

Table 5. Portfolio analysis results for the current situation in Lake Erie and five management scenarios (options) including percent contribution necessary to achieve each option and statistics used to evaluate portfolio efficiency.

	Percent contribution (%)					Portfolio statistics			
Options	Maumee	Sandusky	Detroit	Reef	Total	Risk	Return	Sharpe	Efficient
Current	3	0	4	93	100	1.475	0.454	0.3076	No
1 Opt Return	32	15	30	23	100	1.475	0.728	0.4937	Yes
2 Opt Risk	53	14	8	25	100	1.027	0.454	0.4423	Yes
3 Opt Port	35	15	27	23	100	1.392	0.688	0.4944	Yes
4 Inter-1	4	3	7	86	100	1.436	0.493	0.3436	No
5 Inter-2	10	7	18	66	100	1.403	0.608	0.4331	No

Table 6. Total production from enhanced river stocks necessary to achieve each management scenario (options) and the relative magnitude of change (Fold change) compared to current stock specific contributions.

	Enhanced production (millions of larvae)					Fold change in production			
Options	Maumee	Sandusky	Detroit	Reef	Total	Maumee	Sandusky	Detroit	Reef
Current	39.57	2.00	45.24	1087.08	1173.90	0	0	0	0
1 Opt Return	1531.25	693.41	1406.67	1087.08	4718.42	39	346	31	0
2 Opt Risk	2328.19	624.49	340.98	1087.08	4380.75	59	312	8	0
3 Opt Port	1654.05	682.79	1241.11	1087.08	4665.04	42	341	27	0
4 Inter-1	52.51	34.32	92.22	1087.08	1266.13	1	17	2	0
5 Inter-2	165.51	108.19	290.70	1087.08	1651.48	4	54	6	0

ratios of 0.3436 and 0.4331, respectively. Intermediate options and the associated proportionally smaller increases in production from the Maumee (1 and 4 fold), Sandusky (17 and 54 fold), and Detroit (2 and 6 fold) river stocks could provide initial measurable goals for an adaptive management approach (Williams 2011).

DISCUSSION

Maintaining portfolio effects in multi-stock populations to establish stability and resilience in fisheries resources can be an important consideration for management agencies. In Lake Erie's walleye population, portfolio effects were evident in terms of larval production; however, the current buffering capacity proved to be inefficient, owing to the open-lake reef stock dominating production. Similar to other populations occurring over large spatial scales with complex stock structures (Winemiller and Rose 1992), environmental variability differentially affect Lake Erie walleye stocks generating portfolio effects. However, in Lake Erie walleye, anthropogenic stressors such as harvest and habitat modification may have disproportionate negative effects on river stocks relative to the open-lake stock, causing a deficiency in naturally developed portfolio effects. This type of deficiency leaves a population with complex stock structure susceptible to continued exploitation, natural fluctuations in regional weather patterns as well as the unpredictable effects of climate change (Smedbol and Stephenson 2001, Hilborn et al. 2003, Crozier et al. 2004, Carlson and Satterthwaite 2011). Fortunately, when sufficient data are available, portfolio theory offers a framework for quantifying the relationships among stocks that can lead to better-informed management of multi-stock populations such as Lake Erie walleye.

Differential responses of Lake Erie's local spawning stocks to regional weather conditions are likely responsible for variable production patterns among them, partially driving portfolio effects. For instance, large precipitation events that lead to enhanced discharge from and sediment concentrations in the Maumee and Sandusky rivers (Richards 1990, Richards et al. 2008) may negatively affect larval walleye production in the rivers proper through scouring effects (Mion et al. 1998). However, sediment laden plumes may simultaneously benefit larval walleye production on the open-lake reefs by providing nutrient-rich, turbid waters that offer both ample foraging opportunities and protection from predators (Ludsin et al. 2010; also see Pangle et al. 2012, Carreon-Martinez et al. 2014). As a further contrast, larval walleye produced in the Detroit River are unlikely influenced by regional precipitation because river flows are sourced mainly from Lake Huron and remain stable under precipitation extremes (Pritt et al., *unpublished manuscript*). Unlike riverine production areas, strong wind events can cause high mortality and reduce production in western Lake Erie's open-lake reef complex by dislodging incubating eggs and early yolk sac larvae (Roseman et al. 2001). Additionally, water temperatures in each larval production area respond differently to regional air temperature (Pritt et al., *unpublished manuscript*), which can influence spawn timing, incubation, and hatch rates. As we observed in the 2012, an unseasonably warm spring, peak hatching from the Maumee and open-lake reef stocks shifted dramatically to earlier production, whereas the timing of Sandusky and Detroit River production remained relatively unchanged; although, production from the Sandusky River appeared to be temporally diverse across most years. Therefore, diversity in spawning stocks and their differential response to regional weather conditions produced variability in timing and location of Lake Erie larval walleye production, contributing to portfolio effects.

Portfolio effects can operate at multiple stages of individual development and diversity in multi-stock production is beneficial because it distributes the risk of failed recruitment over larger spatial and temporal scales. In Lake Erie, each stock considered in isolation is limited in spatial scale, while range and variability in temporal production also differs. Upon production, wind- and water-driven open-lake currents transport larval fish to nursery habitats, but transport patterns from each system are annually variable (Fraker et al. 2015). Similarly, the mosaic of open-lake habitat conditions are variable and the overlap between transport and habitat can influence larval growth and presumably survival (Roseman et al. 2005, Houde 2008, Fraker et al. 2015). Zhao et al. (2009), for example, demonstrated the risk of production from a single spatiotemporal window. In this study, prevailing offshore winds that advected open-lake reef larvae away from nearshore nursery habitats corresponded with poor recruitment in 1995 and 1998, likely due to low survival from the dominant producing stock. Walleye recruitment in the overall population is highly variable (Vandergoot et al. 2010), and likely tied to the success or failure of the open-lake reef stock (Busch et al. 1975). Unfortunately, the most temporally dynamic (Maumee and Sandusky rivers) and broadly transported (Detroit River, Fraker et al. 2015) stocks produce relatively few larvae compared to the reefs. Consequently, increasing production from river stocks would increase spatiotemporal diversity in larval fish production and transport (Fraker et al. 2015), thereby improving the probability that more fish experience habitat conducive for growth and survival (Mertz and Myers 1994, Marteinsdottir et al. 2000*a*, *b*). In turn, more stable annual recruitment patterns are likely to emerge relative to dominance by the open-lake reef spawning stock. Improving population stability and resilience begins with identifying naturally evolved reproductive strategies and limiting anthropogenic impacts to maintain the underlying buffering mechanism.

Conventionally, portfolio analyses are performed with many stocks evaluated over a long period; herein we have used relatively few stocks over a short period, which may not have captured the full complexity of Lake Erie walleye dynamics. However, we believe that the results derived from our portfolio analysis are reasonable, given the data used and some of the conservative assumptions made. Larval fish data, used herein, represent the most thorough information available on individual stock components of Lake Erie's walleye population. Although we recognize that our estimates of annual larval fish production are imperfect, we believe that the relative relationships between the stocks presented herein are reasonable approximations of true stock dynamics. As an example, conventional wisdom suggests that the open-lake reef stock is the largest component of Lake Erie's adult population, which was estimated as ~27 million in 2011 (WTG 2014). A recent study that focused on the Maumee River spawning stock, estimated abundance to be 651 thousand individuals (Pritt et al. 2013), representing 2.4% of the estimated adult population size. The similarity in this value to the average ratio of estimated Maumee River larval walleye production to total larval production (3.6%) over our study periods suggests that the relative magnitude of our larval production estimates are reasonable. In addition, given the short time scale and few stocks involved in our analysis, our use of the constant correlation model represents a conservative approach to assessing correlation between stocks and portfolio effects.

While our use of portfolio theory provides an informative evaluation of management options for Lake Erie walleye and an applicable framework for other multi-stock populations, we recommend that future research better account for uncertainty (e.g., Moore et al. 2010). The need to propagate uncertainty in our study was minimal, given the order of magnitude difference in production between the reefs and other spawning locations, as well as the degree of production enhancement needed in the rivers to balance the portfolio. However, in other systems, with potentially more balanced portfolios, propagating all uncertainty components would help identify appropriate management targets, and quantify expectations for a given management action.

Portfolio analysis can identify strengths and weaknesses in multi-stock population structures and help inform rehabilitation or preventative conservation measures. This application of portfolio theory suggests that larval walleye production is currently inefficient, and that enhanced production from riverine stocks would lead to more stable annual production within the broader population. Although maximizing risk for the current return (Option 1) or maximizing return for the current risk (Option 2) would lead to efficient portfolios, the optimized risk and return portfolio (Option 3) may be the most beneficial management strategy for Lake Erie's walleye population. Unfortunately, the levels of production necessary to achieve Option 3 are orders of magnitude greater than current production from these production areas. This option may perhaps be an unrealistic target without major investment in mitigating spawning habitat degradation and solving river-to-lake connectivity issues that currently plague Lake Erie's riverine stocks (Mion et al. 1998, Cheng et al. 2006, Gillenwater et al. 2006, Bennion and Manny 2011). If the current and continued cultural demands on these systems preclude sufficient habitat (and hence, stock) rehabilitation in western Lake Erie's spawning tributaries, then management options 4 and 5 may offer the next best targets for optimal production dynamics, as both seem attainable. Managers could view these options as adaptive management steps (Williams 2011) where, once a production target is achieved, an assessment of recruitment response and management costs could inform continued habitat rehabilitation or stock development. Used in this context, portfolio theory allows flexibility in the management process while providing discrete targets and a clear direction for management actions.

Identifying the appropriate scale, sequence, and method of rehabilitation efforts is challenging; however, stock-specific (localized) scales that incorporate the spatial and temporal complexities of walleye reproductive strategies may be most effective (Lewis et al. 1996, Bozek et al. 2011). Our analysis identified that the quickest path to balancing the larval production portfolio likely starts with improving production from the Sandusky River. Fortunately, managers are in the final stages of a process leading to the removal of the Ballville Dam (USFWS 2014), which should increase access to spawning habitats (Jones et al. 2003) and improve larval production (Cheng et al. 2006). Removal of this barrier on the most depressed spawning stock could generate immediate dividends to the Lake Erie walleye population. Steps to improve walleye production, as well as other species, from the Detroit River are in progress, as researchers and managers are engaged in construction and monitoring of strategically placed artificial reefs throughout the St. Clair-Detroit River system (Manny et al. 2007, 2010, 2015). Past and current habitat restoration efforts on the Maumee River include a dam removal impact assessment (Mueller 2008) and characterization of habitat quality and extent below the first barriers (B. Schmidt, C. M. Mayer, and E. F. Roseman, *personal communication*). Although the results of these efforts remain uncertain, facilitated barrier passage on other Lake Erie tributaries, such as the Grand River, Ontario, have led to increased stock-specific recruitment and spawner abundance (MacDougall et al. 2007), providing optimism for the riverine stocks discussed herein. Additionally, recognition of stock dynamics and management at ecologically relevant scales (e.g., individual stocks) could help reduce the potential for stock-specific overharvest and loss of stock diversity (Stephenson 1999, Crozier et al. 2004, Hutchinson 2008). Therefore, with our portfolio analysis setting a baseline and continued stock specific monitoring, we will be able to evaluate the success of continued riverine rehabilitation and guide future efforts.

Identifying the best combination of habitat rehabilitation and spawning-stock improvement to increase production requires additional information on the factors that limit production in each system. Although, in this study, we assumed average system values (ROI) were equal, each stock is likely distinct, as spawners and larvae experience unique circumstances within their spawning system. ROI corresponds to the efficiency of spawning effort to produce larvae, which is directly related to habitat quality (Hayes et al. 1996). Production from a high value stock (i.e., many larvae per spawner) may benefit most from harvest management, which would increase the number of adults that spawn. Alternatively, a low value stock (i.e., few larvae per spawner) may benefit most from habitat rehabilitation, which could increase the number of larvae produced by current spawning adults. The ability to ascertain stock values could expedite improvement in the Lake Erie walleye reproductive portfolio, highlighting the benefit of sampling across developmental stages on stock-specific scales.

In large ecosystems such as the world's Great Lakes and oceans, restoring and maintaining the natural buffering capacities that have evolved over time may provide the best management approach in the face of global change. For example, the Bristol Bay, AK *Oncorhynchus nerka* (sockeye salmon) stock complex exhibits high spawning-stock diversity and maintained stable population and harvest levels through a substantial shift in regional climate patterns (Hilborn et al. 2003). Although the population as a whole remained stable, the dominant contributing stocks changed. Conversely, the once diverse Arcto-Norwegian *Gadus morhua* (cod) stocks have been heavily harvested over the past 60+ years (Nakken 1994), likely resulting in erosion of diversity in stock specific reproduction. Consequently, spawning-stock structure has degraded and the population as a whole shows reduced resiliency to a changing climate (Ottersen et al. 2006) and failure of distinct sub-populations to effectively buffer the population (Sundby and Nakken 2008). Similarly, maintenance of naturally developed portfolio effects in our case study would promote stable and sustainable fisheries, while buffering walleye against large-scale changes in climate patterns and harvest.

Portfolio theory provides a powerful tool for management of multi-stock populations that occupy large, spatially heterogeneous systems and experience temporal variation in environmental conditions during the reproductive period (Winemiller and Rose 1992, Hilborn et al. 2003, Moore et al. 2010, Schindler et al. 2010, Carlson and Satterthwaite 2011, Griffith et al. 2014, Schindler et al. 2015). By quantifying interactions among stocks, managers can recognize the value of individual stocks as opposed to the largest current producer(s) (Begg and Marteinsdottir 2002, Hilborn et al. 2003). From our analysis, we recognized the importance of riverine stocks as a buffering component to the dominant open-lake reef stock, and that reduction in riverine stock production may contribute to variable recruitment patterns. We propose that the largest improvement in recruitment stability and population resilience may be achieved through the continued rehabilitation of riverine stocks. Given the value of portfolio analysis to our focal (Lake Erie walleye) population, we encourage the use of this approach in other multi-stock populations. The information gained from a portfolio analysis can help managers identify critical stock components necessary for understanding population dynamics, help inform where to target efforts aimed at rehabilitating degraded stocks, and identify sensitive or important stocks in need of increased protection. In turn, improved management decision-making that leads to an enhancement of the naturally developed buffering capacity of multi-stock populations could result in more stable and resilient fish populations and fisheries.

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