Nutrient management and structural shifts in fish assemblages: Lessons learned from an Area of Concern in Lake Ontario

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Abstract

1. While total phosphorus (TP) is a critical determinant of freshwater ecosystem productivity, multiple stressors can induce shifts in energy pathways, with profound implications for ecosystem and fishery restoration. The Bay of Quinte (Lake Ontario, Canada) is a Great Lakes nearshore ecosystem that has been historically subjected to a variety of environmental perturbations: cultural eutrophication, low dissolved oxygen, reduced fisheries, climatic extremes, phosphorus (P) abatement, and aquatic invasive species. We used the Bay of Quinte to study how trophic state alterations affect fish assemblages in Great Lakes nearshore environments by examining the response of fish biomass to TP concentration variability in the presence of multiple stressors.

2. Our analysis is based on a 42-year (1972–2013) dataset from the Bay of Quinte for water quality through the food web to fishes. We employed a series of statistical tools that can offer insights into the structural changes induced by the events examined. We first used dynamic linear modelling to detect temporal trends in fish biomass, while accounting for year-to-year TP variability over three spatial segments of the bay. We then developed piecewise regression models to assess the extent to which specific ecological events induced distinct shifts in the fish assemblage. Multiple regression modelling was used to quantify the relative importance of TP, zooplankton, and surface water temperature on fish biomass.

3. Based on gillnets, there were consistent fish biomass changes across the bay with increased biomass before P control (1972–1977), declines after P control followed by the establishment of a steady state or modest increase (1978–1994), and a declining trajectory during the recent period (1995–2013). Even when accounting for the role of water temperature and zooplankton, TP still had a significant effect on fish biomass. However, the strength and nature of the relationship varied among fish groups, and overall, the effect of TP on fish biomass has weakened in recent years.

4. Our models show that fish biomass in the Bay of Quinte is shaped by the year-to-year TP variability. However, the relationship between P and fish abundance has been modulated by various ecological events with the consequence that the Bay
of Quinte fish assemblage has changed and the food web now produces less fish biomass per unit of TP. A projected reduction of mean ambient TP levels from 30 to 25 μg/L, is expected to induce a 24% decline in total fish biomass, and further shift the fish assemblage with the biomass of planktivores and walleye declining by >60% and 30%, respectively.

5. Recreational fishing provides important economic benefits in the Bay of Quinte, through tourism and other local business operations. Recognising the economic importance of fishing, our analysis provides critical insights regarding the on-going management efforts to reduce external nutrient loadings (point and non-point sources, urban storm water) and further lower ambient TP levels and primary productivity. The potential implications of already low nutrient concentrations for fish productivity represent a major challenge in effectively balancing water quality with fisheries management in the area.

**KEYWORDS**
Bay of Quinte, dreissenid invasion, fish biomass, oligotrophication, phosphorus

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**1 | INTRODUCTION**

Increased nutrient loading from anthropogenic activities has long been recognised as a leading cause of impairments in the Great Lakes ecosystem. The Great Lakes Water Quality Agreement (GLWQA) between Canada and the U.S.A. initiated major management actions in the early 1970s, including mandated improvements in the treatment of sewage wastewater and reduction of point-source phosphorus (P) loading (Auer et al., 2010; Higgins, Hecky, & Guildford, 2008). Restoration efforts have been successful in controlling the external P loading, thereby triggering a process known as re-oligotrophication at many sites across the Great Lakes. Long-term trends of eutrophication-related variables conclusively showed that ambient P and primary productivity have declined to levels that may undermine pelagic ecosystem integrity in the offshore waters around the Great Lakes; the so-called *offshore desertification* (Dove, 2009; Dove & Chapra, 2015).

 Ambient P variability can profoundly affect ecosystem function via bottom-up control (Jeppesen, Jensen, Sondergaard, Lauridsen, & Landkildehus, 2000; Jeppesen et al., 2005), and has been shown to be an important predictor of fish production (deBruyn, Marcogliese, & Rasmussen, 2003; Downing & Plante, 1993; Randall, Kelso, & Minns, 1995). Paired with external stressors (e.g. species invasion, climate change), both eutrophication and re-oligotrophication affect ecosystem productivity (Stockner, Rydin, & Hyenstrand, 2000), as well as the structure of aquatic communities, including plankton, benthos, and fish (Ludsin, Kershner, Blocksom, Knight, & Stein, 2001; Nalepa, Fanslow, & Lang, 2009; Pothoven & Madenjian, 2008). Multiple stressors can induce structural shifts into new complex energy pathways and prevent the restoration of historic fisheries conditions. For example, one of the leading causes of nearshore eutrophication problems in the Great Lakes involves the invasion of zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels in the mid-1990s (Chapra & Dolan, 2012; Fahrenstiel, Bridgeman, Lang, McCormick, & Nalepa, 1995; Johengen, Nalepa, Fahrenstiel, & Goudy, 1995; Ozersky, Evans, & Ginn, 2015; Shimoda et al., 2016), which have been responsible for the altered P cycling and bioavailability (Mclaas, 1996; Strayer, Caraco, Cole, Findlay, & Pace, 1999; Vanderploeg et al., 2002), as well as the diversion of energy from pelagic to benthic habitats and subsequently to the upper trophic levels (David, Davis, & Hunter, 2009; Hecky et al., 2004; Higgins & Vander Zanden, 2010; Nalepa, Fanslow, Lansing, & Lang, 2003).

The Bay of Quinte in Lake Ontario, Canada, is a typical example of a nearshore system within the Laurentian Great Lakes that has been subjected to a wide variety of environmental perturbations (e.g. cultural eutrophication, re-oligotrophication, exotic species invasion). Cultural eutrophication escalated after the 1940s and peaked by the end of the 1960s, seriously affecting water supplies, recreational opportunities, sport, and commercial fisheries in the bay (Kim et al., 2013; Minns, Moore, & Seifried, 2004; Nicholls, Heintsch, & Carney, 2002). Increased phytoplankton abundance decreased underwater light penetration, which in turn reduced the abundance of submerged aquatic vegetation. Low oxygen availability (<2 mg dissolved oxygen/L) critically reduced the habitat of important commercial fish species, thereby destabilising the fish community. Consequently, the commercial fishery in the area was restricted to tolerant fish species such as alewife (*Alosa pseudoharengus*), white perch (*Morone americana*), yellow perch (*Perca flavescens*), rainbow smelt (*Osmerus mordax*), and brown bullhead (*Amiaurus nebulosus*), instead of the previously available popular commercial and sport fish species, e.g. lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedi*), and walleye (*Sander vitreus*), while recreational fishing practically disappeared in the bay during the early 1970s (Johnson & Hurley, 1986).
The winter of 1978 is regarded as the start of P control in the Bay of Quinte, when ambient total P (TP) dramatically declined as tertiary wastewater treatment plants began operation. The fish community shifted, with a significant increase in walleye, while alewife and gizzard shad (*Dorosoma cepedianum*) populations declined (Hoyle et al., 2012). In 1994, dreissenids were first observed in the bay. Post-1994, the Bay of Quinte experienced a regime shift (Currie & Frank, 2015; Nicholls, Hoyle, Johannsson, & Dermott, 2011) with significant improvements in water transparency, which in turn facilitated the re-emergence of macrophytes and a dramatic increase in the abundance of sunfish species, e.g. pumpkinseed (*Lepomis gibbosus*), bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and largemouth bass (*Micropterus salmoides*), whereas walleye, white perch and alewife populations declined (Hoyle et al., 2012). In 1999, round goby (*Neogobius melanostomus*) invaded (Dietrich, Morrison, & Hoyle, 2006), reaching fairly high abundance levels after a short transitional period (Hoyle et al., 2012).

Temporal changes in ambient TP concentrations along with the occurrence of important ecological events in the Bay of Quinte offer a unique opportunity to study how trophic alterations affect the nature of fish assemblages in nearshore environments in the Great Lakes. In this study, our objective is to characterise the spatiotemporal changes in fish biomass in response to TP concentration variability (hereafter referred to as the P2F relationship). Our analysis is based upon a uniquely rich dataset and a series of statistical tools that can offer insights into the structural changes induced by the events examined. We first used dynamic linear modelling (DLM) to detect temporal trends in fish biomass, while accounting for year-to-year TP variability over the three spatial segments of the bay. The key feature of this approach is its flexible structure with year-specific regression coefficients (slopes, intercepts), and thus, no assumption is made about the timing of events or their subsequent effects on the relationship between P and fish biomass. Without postulating any patterns prior to the analysis, we allow our data-driven models to delineate any non-monotonic trends and distinct changes in the fundamental trophic relationships characterising the Bay of Quinte ecosystem. We then develop piecewise regression models to offer complementary information, by assessing the extent to which specific ecological events have (on average) induced distinct shifts in the fish community. The final step of our analysis aims to elucidate the relative importance of TP/chlorophyll *a* (chl-*a*), zooplankton, and surface water temperature on fish biomass variability in the Bay of Quinte.
2 | METHODS

2.1 Study site-dataset description

The Bay of Quinte is located on the north-eastern shore of Lake Ontario (Figure 1). It is a 64 km long Z-shaped embayment with a maximum width of 3.5 km and an area of 254 km². Morphologically, the bay can be delineated into three distinct zones; the upper (35 km), middle (13 km), and lower (16 km) bays. The lower bay is connected with Lake Ontario through two passages at opposite ends of Amherst Island in the south. The bay drains an 18,200 km² catchment area in the north, mostly by the Trent, Moira, Salmon, and Napanee Rivers. The Bay of Quinte is one of 43 degraded sites around the Great Lakes designated as an Area of Concern in 1986 by the International Joint Commission under the GLWQA. Point-source P loading control led to a distinct improvement in water quality conditions by the late 1970s (Minns, Moore, Doka, & St John, 2011). Seasonal mean TP concentrations were over 80 μg/L in the upper bay during the 1960s, declining to 30–40 μg/L after the late 1980s. However, ambient TP concentrations in late summer (August–September) still exceed the level of 30 μg/L. Because the same time of the year coincides with local river flows declining to their lowest annual levels, this recurring pattern was connected to the role of internal nutrient sources (e.g. sediment reflux; Zhang et al., 2013). Recent modelling highlighted internal recycling as one of the key drivers of P dynamics in the bay. In particular, although Trent River flow is the dominant driver of upper bay dynamics, sediment diagenesis processes together with macrophyte and dreissenid activity may be responsible for a significant P release (Arhonditsis et al., 2016).

Long-term and intensive fish community sampling programmes were first initiated on the Bay of Quinte in the late 1950s (Hurley, 1986a). The present analysis draws on catch data from gillnet and bottom trawling from 1972 to 2013. Gillnet sampling began in 1958, but only one site (Hay Bay in the middle Bay of Quinte) was sampled until 1972 when more sites (along with a second gear type, bottom trawl, see below) were added to extend coverage to the entire bay. All gillnet samples come from bottom sets at fixed locations. Seasonal gillnet sets were conducted in some years, but only summer catches were used in this analysis. Generally, gillnets consisted of a graded series of mesh sizes from 38 to 127 mm, stretched mesh in 13 mm increments for a total of eight panels in a single gillnet gang. The range of mesh sizes was suitable for a wide variety of fish species and sizes but was not effective at capturing very small species (e.g. cyprinids) or young-of-the-year. Gillnet mesh was made from multifilament material prior to 1992 and with monofilament thereafter. Paired gillnets with both materials were set in 1991, allowing conversion factors to be calculated (simple linear regression) for major species. Prior to 1992, individual mesh panels were 22.9 m (small mesh sizes) or 45.8 m (large mesh sizes) in length, but all panels were shortened to 15.2 m thereafter. Catches were standardised to 15.2 m of each mesh size for the entire time-series. Since 1992, 140- and 152-mm mesh sizes were added to the gillnet gang but catches from these mesh sizes were not used in the current analysis. Catches for each gillnet gang were summed across mesh sizes.

Bottom trawling has been conducted annually since 1972, except for 1989, using a 3/4 Western bottom trawl at several fixed offshore locations, generally corresponding to the gillnet sites. The trawl has a 13-mm mesh cod-end and most effectively sampled small fishes and young-of-the-year. Only summer bottom trawl catches were used in the analysis. Catches were standardised for the entire time series as total number of individuals per 6-min trawl duration, covering approximately 400 m linear distance and 0.2453 ha in area (Hurley, 1992). Detailed sampling methods have been reported by Hurley (1986a).

Dynamic linear modelling (see following section) was based on the biomass of all species captured in both gillnets and bottom trawls for each year and all three sections of the bay separately. For the rest of the analysis, we pooled gillnet data from the upper and middle sections of the bay. We classified all species into groups based on trophic relationships and economic importance (Supporting Information Table S1). We then estimated group-specific annual average biomass in g/m² of gillnet catch (e.g. planktivores, benthivores, piscivores, percoids, and sunfishes) by summing the mass of all planktivorous, benthivorous, piscivorous, percoids, and centracanthid fishes captured. Fishes of high economic and recreational value (e.g. walleye, yellow perch), and those dominating the samples throughout the study period, e.g. brown bullhead, freshwater drum (Aplodinotus grunniens), and white perch, were also considered separately.

We used growing-season (May–October) averages of TP and chl-a concentrations as two indicators of trophic status, based on samples collected from four stations at Belleville, Napanee, Hay Bay and Conway with weekly frequency from 1972 to 1982 and biweekly frequency thereafter (Currie & Frank, 2015). Chemical analyses (automated, colorimetric) were performed by the Laboratory Services Branch of the Ontario Ministry of Environment, Conservation and Parks. Detailed description of field and laboratory methods for TP and chl-a concentrations were provided by Robinson (1986). Two other independent variables were zooplankton dry weight biomass (mg/m³) and surface water temperature (°C) both obtained through the Project Quinte monitoring programme (Cooley, Moore, & Gelling, 1986). Samples were collected with variate frequency from Belleville, Hay Bay, and Conway (Currie & Frank, 2015); mostly during the ice-free season from early to mid-May until late October, resulting in a total of 17–23 (1975–1982) or 9–12 (1982–2008) samples per station and year (Bowen & Johannson, 2011).

2.2 Modelling framework

Our approach involves three independent steps aiming to detect the temporal trends of fish biomass, while accounting for year-to-year TP variability over the three spatial segments of the bay (Step I: DLM); to detect any abrupt shifts (or change-points) in the time-series of the biomass of trophic guilds (or individual fish species) as a result of the point-source control (1978) and dreissenid invasion (1994) (Step II: piecewise regression modelling); and to quantify the
relative importance of TP, zooplankton, and surface water temperature on fish biomass in the Bay of Quinte (Step III: multiple regression modelling).

2.2.1 Step I: Dynamic linear modelling

The first step of our analysis was based on DLM to delineate the temporal fish biomass trends, while explicitly accounting for the fact that fish biomass typically co-vary with ambient TP concentrations. To examine the relative influence of ambient TP levels on fish biomass, we ran DLM for each gear type and spatial segment of the bay separately. The main components of our DLMs are provided in the following observation equation and subsequent system equations:

**Observation equation:**

\[
\text{ln}[\text{Fish Biomass}]_t = \text{level}_t + \alpha_g \text{ln}[\text{Total Phosphorus}]_t + \epsilon_t \sim N(0,\sigma^2)_t
\]

**System equations:**

\[
\begin{align*}
\text{level}_t &= \text{level}_{t-1} + \text{rate}_t + \alpha_{g1}\;\;\; \alpha_{g1} \sim N(0,\Omega^2_{g1}) \\
\text{rate}_t &= \text{rate}_{t-1} + \alpha_{g2}\;\;\; \alpha_{g2} \sim N(0,\Omega^2_{g2}) \\
\alpha_g &= \alpha_{g1} + \alpha_{g3}\;\;\; \alpha_{g3} \sim N(0,\Omega^2_{g3}) \\
1/\Omega^2_{g1} &= \phi^{-1}(1/\Omega^2_{g1})\;\;\; 1/\psi^2_{g1} = \phi^{-1}(1/\psi^2_{g1}) \quad t > 1; j = 1,2,3 \\
\text{level}_t,\text{rate}_t,\alpha_g &\sim N(0,10,000) \;\; t = 1 \\
1/\Omega^2_{g1} &\sim G(0.001,0.001)
\end{align*}
\]

where \(\text{ln}[\text{Fish Biomass}]_t\) is the measured fish biomass at year \(t\) in spatial segment \(i\) with a given gear type; \(\text{level}_t\) is the mean fish biomass and segment \(i\) at year \(t\) after parsing out the covariance with TP concentrations; \(\text{ln}[\text{Total Phosphorus}]_t\) is the measured (standardized) total phosphorus concentration in year \(t\) and segment \(i\); \(\text{rate}_t\) is the rate of change in mean fish biomass at year \(t\) and segment \(i\); \(\alpha_g\) is the total phosphorus (regression) coefficient; \(\epsilon_t, \alpha_g\) are the error terms for year \(t\) and segment \(i\) sampled from normal distributions with zero mean and variances \(\psi^2_{g1}, \Omega^2_{g1}\) respectively; \(\phi\) is the discount factor representing the aging of information with the passage of time; \(N(0,10,000)\) is the normal distribution with mean 0 and variance 10,000; and \(G(0.001,0.001)\) is the gamma distribution with both shape and scale parameters of 0.001. The prior distributions for the parameters of the initial year \(\text{level}_t, \alpha_g, \text{rate}_t, 1/\Omega^2_{g1}, 1/\psi^2_{g1}\) are considered “non-informative” or vague.

Based on Bayes’ theorem, the sequential DLM updating makes a forecast for time \(t\) using prior knowledge (e.g. literature information, observations at time \(t-1\) or earlier) on model parameters and data observed at time \(t\) (Mahmood, Bhavsar, & Arhonditsis, 2013). The discount factor is applied to this iterative process, such that older observations are weighted less than newer ones. Discount factors between 0.8 and 1.0 were examined during the specification of our modelling framework. We identified a value of 0.95 that optimally balances performance (e.g. deviance = -2log [likelihood] ) with uncertainty of the year-specific estimates of the stochastic nodes (such as regression coefficients, rates of change, fish biomass corrected for the TP variability) as well as the error terms. Specifically, we selected the discount factor that resulted in the highest model performance, while ensuring the highest degree of identification, as expressed by the coefficient-of-variation values of the dynamic model parameters (Visha, Gandhi, Bhavsar, & Arhonditsis, 2015). A discount factor of 0.95 stipulates that the precision of each stochastic node within a given year is reduced by 5% relative to the precision assigned to the same parameter for the previous time step.

2.2.2 Step II: Piecewise regression modelling

The second phase of our analysis is based on piecewise regression models to detect any abrupt shifts in the time-series of fish biomass potentially triggered by two events: nutrient point-source P control (late 1970s) and a regime shift (mid-1990s). The piecewise regression model was formulated as follows:

\[
\text{ln}[\text{Fish Biomass}]_t = \beta_0 + \beta_1 \text{ln}[\text{TP}]_t + \beta_2 (t-1972) 1972 \leq t < 1978 + \beta_3 (t-1978) 1978 \leq t < 1995 + \beta_4 (t-1995) 1995 \leq t < 2014 + \epsilon_t \quad \epsilon_t \sim N(0,\sigma^2)
\]

\[
\beta_i \sim N(0.00001) = 0.123.4
\]

\[
1/\sigma^2 \sim G(0.001,0.001)
\]

where \(\text{ln}[\text{Fish Biomass}]_t\) is the measured fish biomass in year \(t\); \(\beta_0\) is the intercept; \(\beta_1\) is the TP (regression) coefficient; \(\text{ln}[\text{TP}]_t\) is the measured TP concentration in year \(t\) (expressed in natural logarithmic scale); \(\beta_2, \beta_3,\text{and} \beta_4\) represent the slopes (or rates of fish biomass change) for the period between the beginning of the study period and prior to point-source control (1972-1977), after point-source control and before the dreissenid invasion and potential regime shift (1978–1994), and after the dreissenid invasion (1995–2013), respectively.

2.2.3 Step III: Multiple regression modelling

The next phase of our analysis examined the relative role of TP, zooplankton biomass, and surface water temperature on fish biomass. Our multiple regression models were formulated as follows:

\[
\text{ln}[\text{Fish Biomass}]_t = \beta_0 + \gamma_1 \text{ln}[\text{Zooplankton}]_t + \gamma_2 \text{ln}[\text{TP}]_t + \gamma_3 \text{ln}[\text{Surface Water Temperature}]_t + \epsilon_t \\
\epsilon_t \sim N(0,\sigma^2)
\]
where $\ln [\text{Fish Biomass}]$, is the measured fish biomass in year $t$, $\ln [\text{Zooplankton}]$, $\ln [\text{TP}]$, and $\ln [\text{Surface Water Temperature}]$, are the average zooplankton biomass, TP concentration, and surface water temperature in year $t$; $\gamma_1$, $\gamma_2$, and, $\gamma_3$ are the corresponding regression coefficients; and $\gamma_0$ is the intercept of the relationship. With a second set of multiple regression models, we examined the signature of phytoplankton biomass, expressed as chl-α concentrations, on year-to-year variability of fish biomass, instead of TP.

We did not use the dreissenid biomass data directly in our modelling analysis, because they were inconclusive with respect to their spatiotemporal patterns in the system (Dermott and Bonnell, 2011; Project Quinte, Monitoring Report #20). In particular, except from a general increasing trend since the mid-1990s, there is considerable year-to-year variability in each of the sites examined, whereas the measurement error is fairly high and comparable with the actual average values (Supporting Information Figure S1). In fact, the coefficient-of-variation associated with the dreissenid biomass is approximately equal to (or even greater than) 100%. More importantly, even if the dreissenid data were more conducive to detecting statistically significant relationships, our analysis at its very essence does not solely focus on their direct impact on fish assemblages, but also on indirect effects and the restructuring of system trophodynamics, whether from dreissenids or other effects during this recent time period. If we also consider the wide array of abiotic factors and trophic linkages modulating the effects of dreissenids on fish, our modelling work represents a pragmatic strategy to capitalise upon the available information at hand.

The objectives of our study also bear resemblance to those addressed by Hoyle et al. (2012); however, their study was based entirely on prespecified time-stanzas (1969–1977, 1978–1994, 1995–2002, 2003–2009) which were compared with analysis of variance to identify statistically significant differences in the fish community over time. Our study extends the previous work in the following three directions: (1) we examine fish trends in time and space without any prior temporal binning (DLM), thereby allowing the identification of non-monotonic patterns and potential stationary or inflection points in the time series; (2) we delineate the signature of important covariates (dynamic, piecewise, and multiple regression modelling), such as TP/chl-α, zooplankton, and surface water temperature on fish biomass; and (3) we develop risk assessment tools that can be directly used to guide fisheries and water quality management in the Bay of Quinte area.

3 | RESULTS

Fish biomass, derived from gillnet data, demonstrated consistent patterns across the three sections of the bay (Figure 2a–c). In the upper bay, fish biomass increased until the early 1980s, followed by a gradual decline (Figure 2a). In the middle bay, fish biomass was characterised by a wax and wane pattern until the early 1990s, followed by a gradual decline (Figure 2b). Fish biomass was fairly constant in the lower bay until the mid-1980s, followed by a distinct increase through the late 1980s and a sharp decline thereafter (Figure 2c). The associated rates of change were suggestive of a weak increase in all three sections during the initial years, switching to weakly decreasing rates of change after the late 1980s (Figure 3a–c). In particular, the posterior distributions that represent our knowledge of the rate parameters indicate average odds of 2.67:1 that the rates of change in the upper bay were greater than one (fish biomass increase) during the early years of the study and 2.04:1 that the rates of change were lower than one (fish biomass decrease) during the latter years. (The odds ratio of the rate parameter being below one in a particular year is the ratio of the probability mass below one to the mass above one.)

Counter to the fish biomass estimates derived from gillnets, data from bottom trawls reflected low biomass levels throughout the study period across all sections of the bay (Figure 2d–f). In the upper bay, predicted fish biomass levels increased until the mid-1970s followed by a steep decline until the early 1980s and remained fairly constant thereafter (Figure 2d). The middle bay was characterised by a rapid drop during the early years of the study period and then gradually increased until the early 1990s, and was subjected to year-to-year variability with no apparent long-term trend during the rest of the study period (Figure 2e). In the lower bay, fish biomass exhibited a minor initial increase that declined until the early 1980s and then remained low throughout the study period (Figure 2f). Notably, there were a couple of excessively high fish biomass estimates from the bottom trawls (e.g. middle bay in 1981 and lower bay in 2001); possibly due to sampling bias/error associated with high catches of schooling fish. There were no profound changes in the rates of change in fish biomass levels across the three segments (Figure 3d–f), which fluctuated around the level of a steady trend ($rate_t = 1$) throughout the study period. Specifically, the posterior distributions for the rate parameters were characterised by odds ratios that were never greater than 1.75:1, for either increasing ($rate_t > 1$) or decreasing ($rate_t < 1$) trends, in the three segments throughout our study period. We also examined the strength of the relationship between TP concentrations and fish biomass based on the corresponding (year-specific) standardised regression coefficient values. Our analysis showed that the TP signature on total fish biomass has become distinctly weaker (or even negative) for all three sections of the Bay of Quinte in recent years (Supporting Information Figure S2).

Our piecewise regression modelling reinforced the presence of non-monotonic temporal trends in fish biomass. After we partial out their covariance with year-to-year TP variability (Table 1; Supporting Information Figure S3), there was a distinctly decreasing trend in the recent period for most fish groups, consistent with a strongly negative response to the regime shift and dreissenid invasion. In particular, total fish biomass, as well as the biomass of benthivores, piscivores, percoids, walleye, and freshwater drum increased during the post-P control period, and then exhibited a
steady downward trend (see slope estimates and associated errors in Table 1). Piscivores, percoids, walleye, and freshwater drum decreased until the late 1970s with biomass levels rebounding during the post-P control period (Table 1). Sunfish displayed the opposite pattern, i.e. a positive trend during the pre-P control period, switching to a negative trend post-P control, and then rising again in recent years. Yellow perch demonstrated a statistically discernible declining trend after the regime shift, whereas white perch showed a continuously positive trend with a nearly steady increase since point-source P control.

Fish community composition displayed distinct shifts among three time periods: pre-P control (1972–1977), post-P control (1978–1994), and the recent state (1995–2013). Planktivorous fishes dominated the fish community (c. 59.5%) during the hyper-eutrophic period, followed by benthivorous fishes (33.5%), whereas piscivorous fishes accounted for <7% of the total fish biomass (Figure 4; top panels). Following point-source P control, piscivores increased dramatically in the system, representing approximately 40.5% of the total fish biomass, followed closely by benthivorous fishes (38.8%), while planktivores declined to <20.7% of the standing biomass. Recently, the fish community has been dominated by benthivores (63.1%) followed by piscivores (34%), and a minor fraction of planktivores (<3%). Within the dominant fish species, walleye increased from 5.4 to 44.4% post-P control and then declined to 20.4% (Figure 4; bottom panels). White perch demonstrated the opposite pattern, as they declined from 63.8 to 23.7% post-P control, followed by a modest relative increase to 25.7%. Yellow perch declined from 23.1 to 16.3% post-P control, and then went up to 27.1%. Sunfish species have recently demonstrated an increase (c. 2%). Brown bullhead and freshwater drum were consistently present in the fish assemblage of the Bay of Quinte. The rest of the fish species of the Bay of Quinte exhibited a gradual increase across the time periods studied.

We also developed multiple regression models to examine the relative importance of ambient TP concentration (Supporting Information Figure S4), zooplankton biomass (Supporting Information Figure S5), and surface water temperature (Supporting Information Figure S6) on fish biomass in the bay. The posterior parameter patterns (i.e. signal-to-noise or mean-to-standard deviation ratios) provide evidence that year-to-year variability of TP concentrations is an influential regulatory factor, even when the role of zooplankton and surface water temperature on fish biomass is taken into account (Table 2). However, the strength and nature of this relationship varied significantly among the different fish groups examined. In particular, the strongest positive signature of TP variability was
evident on the biomass of planktivores, walleye, brown bullhead, and percoids (Table 2). By contrast, sunfish and freshwater drum were characterised by a strongly negative relationship with ambient TP levels. Zooplankton had a strongly positive signature on the biomass of walleye, percoids, piscivores, and freshwater drum, but its role was weakly identified with the rest of the fish groups examined (Table 2). The effects of surface water temperature on fish biomass were weak, except for brown bullhead and sunfish biomass, which were characterised by strongly negative and positive relationships, respectively. Similar inference is drawn from the multiple regression models in which we used chl-a as a predictor variable (Supporting Information Figure S7), although it is worth noting that the linkage between sunfish and zooplankton is more clearly manifested with the latter model (Supporting Information Table S2).

Finally, we applied our multiple regression models to predict the fish biomass of four different groups at various ambient TP concentrations under average zooplankton biomass and surface water temperature (Figure 5a–d; Table 3). Namely, a reduction of average TP concentration from 30 to 25 μg/L projected an approximate decline of 20% in the median total fish biomass (Figure 5a). The strongest decreasing trend was evident with the predicted distributions of planktivores, which dropped by >60% at TP levels of 25 μg/L (Figure 5b). There was an approximate decline of 20% and 30% in the median biomass values of piscivores and walleye at an average TP of 25 μg/L (Figure 5c). In contrast, the expected median biomass of sunfish went up by 112% with a TP reduction to 25 μg/L (Figure 5d).

4 | DISCUSSION

Our analyses demonstrate that temporal trends in fish biomass in the Bay of Quinte are well explained by TP variability across the whole 42-year time series (1972–2013), even with the occurrence of significant ecological events that potentially confound descriptions of biological change. However, these ecological events are not irrelevant. There have been significant shifts in the fish community as species and functional groups have responded differently to these drivers. Fish biomass has responded to the ecosystem productivity set by TP concentrations, but the production of fish biomass is determined by energy dynamics through the food web, which these ecological events have changed. The consequence is that the Bay of Quinte food web now produces less fish biomass per unit of TP.
TABLE 1  Posterior parameters of the piecewise regression models developed to parse out the signature of total phosphorous (TP) concentrations on fish biomass from the temporal trends during three time periods in the Bay of Quinte: the beginning of the study period until the point-source control (Pre-TP-Ctrl; 1972–1977); after point-source control (Post-TP-Ctrl; 1978–1994); after the invasion of dreissenids and round goby (Recent; 1995–2013)

| Group name    | Intercept | Slope (TP) | Slope (Pre-TP-Ctrl) | Slope (Post-TP-Ctrl) | Slope (Recent) |
|---------------|-----------|------------|---------------------|----------------------|----------------|
| All fish      | Mean      | 3.615      | 0.326               | 0.115                | 0.030          | -0.032         |
|               | SD        | 1.011      | 0.265               | 0.042                | 0.013          | 0.012          |
| Planktivores  | Mean      | -12.260    | 3.973               | 0.308                | 0.029          | -0.072         |
|               | SD        | 3.062      | 0.803               | 0.127                | 0.039          | 0.038          |
| Benthivores   | Mean      | 4.534      | -0.150              | 0.058                | 0.020          | -0.021         |
|               | SD        | 0.736      | 0.193               | 0.031                | 0.009          | 0.009          |
| Piscivores    | Mean      | 4.743      | -0.414              | -0.077               | 0.086          | -0.019         |
|               | SD        | 2.006      | 0.526               | 0.083                | 0.025          | 0.025          |
| Sunfish       | Mean      | 5.259      | -2.009              | 0.046                | -0.044         | 0.086          |
|               | SD        | 3.107      | 0.821               | 0.136                | 0.043          | 0.039          |
| Percids       | Mean      | 8.059      | -1.151              | -0.114               | 0.040          | -0.073         |
|               | SD        | 1.652      | 0.433               | 0.069                | 0.021          | 0.020          |
| Walleye       | Mean      | 7.861      | -1.347              | -0.287               | 0.092          | -0.073         |
|               | SD        | 2.489      | 0.653               | 0.103                | 0.031          | 0.031          |
| Yellow perch  | Mean      | 9.000      | -1.587              | 0.023                | -0.026         | -0.084         |
|               | SD        | 1.504      | 0.394               | 0.062                | 0.019          | 0.019          |
| White perch   | Mean      | -2.721     | 1.468               | 0.065                | 0.065          | 0.044          |
|               | SD        | 1.945      | 0.510               | 0.081                | 0.025          | 0.024          |
| Brown Bullhead| Mean      | 5.815      | -1.446              | 0.251                | 0.018          | -0.110         |
|               | SD        | 1.992      | 0.523               | 0.084                | 0.025          | 0.025          |
| Freshwater Drum| Mean  | 11.550     | -2.793              | -0.282               | 0.065          | -0.030         |
|               | SD        | 2.186      | 0.573               | 0.091                | 0.028          | 0.027          |

FIGURE 4  Observed changes in the fish community composition across three time periods in the Bay of Quinte: the beginning of the study period until the point-source P control (Pre-P-Ctrl; 1972–1977); after point-source P control (Post-P-Ctrl; 1978–1994); and after the regime shift and dreissenid invasion (Recent; 1995–2013). The trophic guilds illustrated in the top panels are presented in Table 1 of the Supporting Information section
Projected consequences of further lowering TP targets is likely to be reduced total fish biomass with further fish community shifts as species differentially respond to changes from TP reductions, with projected biomass decreases in walleye and planktivore and increases in freshwater drum and sunfish.

4.1 What are the spatiotemporal trends of fish populations in the Bay of Quinte?

The Bay of Quinte supports a diverse fish fauna with important recreational and commercial value, and thus the structural shifts of the local fish community induced by cultural eutrophication have been studied since the 1950s (Hoyle et al., 2012). Phytoplankton density, fuelled by nutrient inputs, affected water clarity, macrophyte abundance, zooplankton biomass and composition, and, through microbial decomposition of the excessive biogenic material, oxygen concentrations near the bottom, which ultimately shaped benthic community composition. Consequently, relative changes in the abundance of food along with compromised habitat integrity have been identified as key regulatory factors of the structure of fish assemblages (Hoyle et al., 2012; Koops, Irwin, MacNeil, Millard, & Mills, 2006). The major impacts of eutrophication were associated with a decrease of large piscivores as well as an increase of both planktivorus and benthivorous fish biomass in the bay (Hurley, 1986b; Hurley & Christie, 1977), a result that was also evident in our look at fish community shifts (Figure 4), as well as the piecewise regression modelling results (see corresponding Pre-TP-Ctrl slopes in Table 1). Similar to past studies (Jeppesen et al., 2000; Yurk & Ney, 1989), our analysis highlighted the well-identified positive signatures of TP and chl-α concentrations on planktivorous fish biomass with both the piecewise and multiple regression models. Year-to-year phytoplankton variability is also a fairly strong predictor of fish-benthivorous biomass, whereas piscivores followed closely the inter-annual variability of both phytoplankton and zooplankton abundance and less so the temporal TP trends. In particular, the well-identified positive slope between ambient TP levels and piscivorous biomass, when using zooplankton and surface water temperature as covariates, disappeared when explicitly stipulating a segmented relationship with time. The latter result suggests that other factors more directly linked to the top fish predators, and not year-to-year TP variability alone, can more effectively describe their (nearly) linear responses across the time-stanzas (pre-, post-P control, and recent).

Both piecewise and DLM showed that total fish biomass, based on gillnet samples, closely followed year-to-year TP variability during

| Group       | Slope | Intercept | Total phosphorus | Zooplankton | Surface water temperature |
|-------------|-------|-----------|-----------------|-------------|---------------------------|
| All Fish    | Mean  | −1.053    | 1.601           | 0.291       | −0.070                    |
|             | SD    | 2.208     | 0.487           | 0.238       | 0.093                     |
| Planktivores| Mean  | −23.25    | 6.679           | 0.236       | −0.007                    |
|             | SD    | 6.44      | 1.424           | 0.697       | 0.273                     |
| Benthivores | Mean  | 2.947     | 0.339           | 0.245       | −0.073                    |
|             | SD    | 1.544     | 0.341           | 0.167       | 0.065                     |
| Piscivores  | Mean  | −4.605    | 1.551           | 0.605       | −0.022                    |
|             | SD    | 3.16      | 0.732           | 0.358       | 0.140                     |
| Sunfish     | Mean  | −0.584    | −3.414          | 0.449       | 0.470                     |
|             | SD    | 6.376     | 1.647           | 0.753       | 0.269                     |
| Percoids    | Mean  | −1.910    | 1.712           | 0.476       | −0.144                    |
|             | SD    | 3.028     | 0.668           | 0.327       | 0.128                     |
| Walleye     | Mean  | −3.825    | 2.376           | 0.667       | −0.253                    |
|             | SD    | 4.227     | 0.933           | 0.457       | 0.179                     |
| Yellow perch| Mean  | 1.350     | 0.106           | 0.390       | −0.043                    |
|             | SD    | 3.617     | 0.799           | 0.391       | 0.153                     |
| White perch | Mean  | 0.926     | 0.851           | 0.061       | −0.068                    |
|             | SD    | 3.895     | 0.860           | 0.421       | 0.165                     |
| Brown bullhead | Mean | 3.626 | 1.717           | 0.207       | −0.546                    |
|             | SD    | 5.676     | 1.245           | 0.570       | 0.282                     |
| Freshwater Drum | Mean | 5.761 | −2.768          | 1.421       | −0.074                    |
|             | SD    | 4.224     | 0.933           | 0.457       | 0.179                     |
the pre-P control period (1972-1978) in the shallow upper bay. Taken together, these results primarily reflect the predominance of small-bodied and tolerant fish species, such as white perch (a non-native invertevore), alewife (a non-native planktivore), and gizzard shad (a herbivore). This pattern was reinforced by the absence of controlling interactions with top predators, especially walleye, as their reproduction was probably impaired by poor ambient conditions and/or increased predation on their larval stages by abundant intermediate-sized predators (Hurley, 1986a; Minns & Hurley, 1986). Total fish biomass displayed similar temporal variability across the entire system, but was diminished in the lower bay relative to the upper bay; especially during the eutrophic 1972–1978 period. Given that the lower bay is strongly influenced by wind-driven mixing and intrusions of cold-water masses from Lake Ontario, it stands to reason that there is distinct spatial heterogeneity in ecosystem structure and function. For example, whereas the lower food web experiences seasonal shifts between autotrophs and heterotrophs in the upper bay, the organic carbon pool in the lower bay area is dominated by typical components of the microbial loop (Munawar, Fitzpatrick, Niblock, & Lorimer, 2011). While the likelihood that these differences in

### TABLE 3  Predictions of fish biomass (g per m$^2$ of gillnet) for two total phosphorus (TP) levels, 30 and 25 μg TP/L, under average zooplankton biomass values and surface water temperature in the Bay of Quinte

| Groups          | Fish biomass | TP level (μg/L) | % Change |
|-----------------|--------------|----------------|----------|
|                 |              | 30             | 25       |          |
| All fish        | 92.5 ± 9.3   | 69.6 ± 12.7    | -24.3    |
| Planktivores    | 1.9 ± 0.6    | 0.6 ± 0.3      | -67.0    |
| Benthivores     | 51.2 ± 3.6   | 48.2 ± 6.5     | -5.5     |
| Piscivores      | 28.8 ± 4.4   | 22.1 ± 6.2     | -22.2    |
| Sunfish         | 0.5 ± 0.2    | 1.0 ± 1.0      | 112.8    |
| Percoids        | 35.6 ± 4.9   | 26.4 ± 6.7     | -24.9    |
| Walleye         | 16.4 ± 3.1   | 10.9 ± 3.8     | -32.1    |
| Yellow perch    | 17.7 ± 2.9   | 18.0 ± 6.1     | 1.8      |
| White perch     | 17.1 ± 3.1   | 15.0 ± 5.2     | -10.5    |
| Brown bullhead  | 0.9 ± 0.2    | 0.8 ± 0.4      | -20.0    |
| Freshwater drum | 9.3 ± 1.8    | 15.9 ± 7.8     | 74.5     |

### FIGURE 5  Posterior predictive distributions of fish biomass (g/m$^2$ of gillnet) at different ambient total phosphorous (TP) levels. The distributions depicted for biomass of four important fish groups: (a) all fish, (b) planktivores, (c) walleye, and (d) sunfish. Dashed lines correspond to the posterior medians
the lower food web configuration modulate the fish community structure cannot be ruled out, the general tendency of higher fish biomass in the upper bay probably stems from its morphological features that provide extensive shallow areas, lentic conditions, and warm temperatures (22–25°C) for most of the summer for spawning and feeding (Hoyle et al., 2012).

Our multiple regression models are suggestive of a weak relationship (i.e. poorly identified slopes) between fish abundance and year-to-year variability of surface water temperature. Nonetheless, historical evidence highlights that the observed change in fish populations following the sharp reduction in P inputs and reversal of eutrophication trends was partly confounded by the occurrence of weather extremes (Hoyle et al., 2012). Namely, white perch experienced catastrophic die-offs in 1977–1978, probably associated with a severe winter, followed by an exceptionally strong year-classes of yellow perch and walleye the next spring (Minns & Hurley, 1986). Subsequently, the walleye population recovered to very high levels (Bowlby, Mathers, Hurley, & Eckert, 1991; see also the corresponding positive Post-TP-Ctrl slope in Table 1); the fish community in the bay shifted to dominance by piscivores, effectively controlling the formerly hyper-abundant prey fish species (e.g. alewife) through predation (Ridgway, Hurley, & Scott, 1990). From the late 1970s until the early 1990s, the Bay of Quinte returned to its status as one of the premier walleye fisheries in Canada. Stomach contents of large piscivores in the 1977–81 post-P control period showed that alewife was the most common prey item, with rainbow smelt, yellow perch, and white perch as the next most common food items (see Table 7 in Hurley, 1986a). Abundant walleye may also have prevented yellow perch from continuing to increase in the upper bay following production of its own large 1978 year-class, whereas white perch have gradually recovered but not to the formerly high levels of abundance (see the weakly negative and positive Post-TP-Ctrl slopes for yellow and white perch in Table 1, respectively).

Along with the pressure exerted from top fish predators, inter- and intra-specific competition have been identified as important factors that may have mediated shifts in the fish community (Hoyle et al., 2012). By contrast, little evidence exists in support of the hypothesis that changes in algal composition and biomass, initiated by P control, significantly affected the diets of dominant fish species, such as rainbow smelt, white perch, yellow perch, and alewife (Hurley, 1986b). Empirical evidence from the early 1980s suggested that calanoid and cyclopod copepods still dominated their diets and less so larger macrozooplankton species (e.g. *Daphnia pulex*). Interestingly, the strong reliance of planktivores, white perch, and yellow perch on zooplankton was not manifested in our multiple regression analysis, probably suggesting that total zooplankton abundance may not be the best surrogate variable to establish linkages with the fish community. It is worth noting though that the relationship among zooplankton and planktivores, white perch, and yellow perch becomes significantly stronger ($r^2 = 0.55–0.83$) when using cladoceran biomass as a predictor variable.

### 4.2 What is the impact of recent events on the fish community of the Bay of Quinte?

The recent time period has been an era of rapid change in habitat and food web structure in the Bay of Quinte (Nicholls & Carney, 2011; Nicholls et al., 2002). Increased water transparency is most likely to be the primary causal factor of the extensive proliferation of submerged macrophytes in the system (Leisti, Doka, & Minns, 2012; Seifried, 2002). Macrophyte coverage increased from about 30–40% in the early 1990s to more than 75% by the 2000s (Leisti et al., 2012). Shimoda et al. (2016) reported a profound decrease of spring diatom biovolume, while dreissenid activity could also be responsible for the gradual decline of $N_2$-fixers (*Aphanizomenon* spp. and *Anabaena* spp.) and may be partly associated with the outbreaks of toxin-producing *Microcystis* spp. (Shimoda et al., 2016). Dreissenids can also induce structural shifts in the zooplankton community due to their ability to filter a wide range of particles, including microzooplankton (e.g. protozoa, ciliates, rotifers, veligers, and nauplii). The latter effect can have broader ramifications for the diets and ultimately the integrity of fish populations (Bowen & Johannsson, 2011). Long-term fisheries dynamics are generally linked to shifts in planktonic production, as most fishes directly feed on plankton at some point during their life cycle (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003). Our analysis provides evidence of a decline in total fish biomass as well as the biomass of distinct trophic guilds (planktivores, benthiivores) and commercially important fish (walleye) in response to these ecosystem changes.

A potentially confounding factor in the recent period of our analysis is the invasion of round goby. Round goby were first reported in the Bay of Quinte in 1999 (Dietrich et al., 2006) and their population increased rapidly within the next 3–4 years, followed by a decline in 2004 and subsequent stabilisation at high abundance levels (Taraborelli, Fox, Johnson, & Schaner, 2010). Generally, existing evidence suggests that round goby rapaciously consume eggs of native fishes (Chotkowski & Marsden, 1999; Jude, 2001), may displace native species through shelter monopolisation (Balshine, Verma, Chant, & Theysemeyer, 2005), while their boom and bust dynamics can profoundly modulate benthic communities and nutrient cycles (Bunnell, Johnson, & Knight, 2005; Janssen & Jude, 2001). In the Bay of Quinte, the prey types of greatest importance to round goby are dreissenids, followed by chironomids and zooplankton. Round goby, in turn, are heavily preyed by yellow perch and largemouth bass, and are consumed by all obligate and facultative piscivores in the Bay of Quinte (Taraborelli et al., 2010). Viewed from this perspective, round goby represent a new vector of energy transfer from dreissenids to higher levels in the food web, potentially altering ecosystem trophodynamics (Campbell et al., 2009; Johnson, Allen, Corkum, & Lee, 2005). However, Hoyle et al. (2012), using fish data from 1969 to 2009, provided evidence that fish community changes, after the invasion of round goby, were not as profound as the response to nutrient loading control or dreissenid invasion. The impacts of round goby may require more time to manifest themselves in the food web (Hoyle et al., 2012). Our analysis extended the study...
period until 2013, but we were still not able to identify a major response to the round goby invasion.

In the Bay of Quinte, several hypotheses have been proposed to explain reduced walleye abundances, such as diminished ecosystem productivity, decreased available walleye habitat due to increased water clarity, increased refuges for predators of juvenile walleye due to increased macrophyte cover, and exploitation (Chu, Minns, Moore, & Millard, 2004; Koops et al., 2006; Lester, Dextraise, Kushneruk, Rawson, & Ryan, 2004; Robillard & Fox, 2006). Chu et al. (2004) developed an empirical thermal-optical model based on walleye preferences for cool water and low light intensity. The thermal component of this model was suggestive of a growth limitation (or even cessation) in the upper bay during summer when temperature exceeds 23.5°C for mature walleye and 25°C for immature walleye (Hurley, 1986c). Thus, walleye benefit from migration away from the warmer waters of the upper Bay of Quinte toward the cooler waters of Lake Ontario during summer; a spatial pattern that has not changed with recent ecosystem changes (Bowlby & Hoyle, 2011). The decline in walleye abundance in the upper bay is also consistent with the optical component of the Chu et al. (2004) model, as recent increases in water clarity also triggered the re-emergence of aquatic macrophytes in the nearshore area, which in turn facilitated dramatic increases in the abundance of fish species associated with vegetation, such as bluegill, pumpkinseed, black crappie, and largemouth bass (see the recent positive changes in slope for sunfish species in Table 1). The latter change in the nearshore fish assemblage has been suggested as an important driving factor of the decline in walleye abundance (Bowlby, Hoyle, Lantry, & Morrison, 2010). In the recent time period, walleye diets comprise a greater number of fish species, such as yellow perch, alewife, gizzard shad, and round goby (Bowlby & Hoyle, 2011). Following the ambient TP trends though, smaller forage fish species (e.g. alewife and gizzard shad) have declined in the Bay of Quinte. Hence, the relative contribution of round goby to walleye diet and the potential to meet its nutritional needs may be a key factor to realised growth rates and future trajectories.

4.3 On-going challenges for nutrient management in the Bay of Quinte

One of the recent propositions to further improve prevailing conditions in the Bay of Quinte has been to revisit the targeted TP benchmark (seasonal average of 30 μg TP/L) to delist the system for the beneficial use impairment “Eutrophication or Undesirable Algae” (Arhonditsis et al., 2016). Namely, the upper threshold level is proposed to be 40 μg TP/L, with exceedances less than 10–15% in both time and space. Given that TP concentrations are log-normally distributed in the Bay of Quinte and TP values <15 μg/L are likely to occur only 10% of the time during the growing season, then 10–15% exceedances of the 40 μg TP/L level is similar to adopting a targeted seasonal average of 25–28 μg TP/L (Arhonditsis et al., 2016; Kim et al., 2013). Based on the key findings of the present analysis, the new target raises concerns regarding the implications of lower TP concentrations for the sustainability of fisheries in the Bay of Quinte. Our modelling exercise suggests that a projected reduction of mean ambient TP levels from 30 to 25 μg/L, is expected to bring >20% decline in the median total fish biomass, whereas planktivores and walleye could be reduced by >60% and 30%, respectively. These predictions clearly offer a cautionary perspective on the likelihood of fish biomass to further decline in the Bay of Quinte, but it should also be noted that: (1) they are derived from simple statistical models without the mechanistic foundation to accommodate different aspects of fish behaviour and ecology; and (2) the TP signature on piscivorous fish biomass weakens (or even changes in sign) when we consider a segmented relationship with time (see previous discussion).

Recognising that each fishing gear has unique biases with respect to habitat and species selectivity, our analysis draws upon trend-through-time catch data from both gillnets and bottom trawls with intensive geographic coverage that collectively provide evidence of dramatic shifts in the fish community over 5 decades. Similarly, Hoyle et al. (2012) reported an increase in the proportion of total fish community biomass represented by piscivores from 0.04 to 0.30 in the offshore and from 0.08 to 0.35 in the nearshore between the pre-P and post-P control periods, a decline to 0.15–0.21 post-dreissenids, and an increase to 0.21–0.26 after round goby invasion. Thus, while the current values are greater than the threshold of 0.20, indicative of a balanced fish community (Brousseau & Randall, 2008; Hurley, 1986a), it is important to note that the Bay of Quinte has a long history of abrupt shifts in its food web structure. Viewed from this perspective, our model predictions are defensible and could be realised in the foreseeable future, even if active nutrient regeneration mechanisms in the system compromise the efficiency of additional non-point source loading reductions to improve ambient conditions in the short-term (Arhonditsis et al., 2016; Kim et al., 2013).

A missing piece of knowledge, which is potentially relevant to our modelling projections, is the impact of exploitation on the fish community in the Bay of Quinte. Recreational fishing provides important economic benefits, through tourism and other business operations, such as equipment rentals, supplies, and accommodations for anglers (Ewaschuk, 2005). Earlier estimates (non-adjusted for inflation) of angler expenditures showed that $4 million were spent just on rental accommodations between May and October of 1984 and up to $6 million (non-adjusted) in direct expenditures by open-water anglers (Trushinski, 1986). In 1994, during the peak of the walleye recreational fishery, total expenditure (direct and invested) attributed to walleye angling was estimated to be $11.9 million for the bay (non-adjusted), although the latter amount has decreased to $4.9 million in 2000 due to the decline in walleye (Ewaschuk, 2005). Recognising the economic importance of fishing in the area is equally critical when assessing the ecological implications of human activities, including restoration actions, on fish community sustainability. This exercise is particularly important in view of the on-going management efforts to reduce external nutrient loadings (point and non-point sources, urban storm water) and further lower ambient TP levels and primary productivity (Arhonditsis et al., 2016). This potential conflict between water quality and fisheries management is not
unique to the Bay of Quinte. Across the Great Lakes basin there is interest in further reducing TP targets and concern about the fishery productivity implications of already low nutrient concentrations, especially in offshore areas of the Great Lakes.

In conclusion, our analysis provided evidence that P2F relationships can be significantly modulated by the combined effects of stressors that exert continuous pressure (e.g. exploitation and eutrophication) as well as abrupt disturbances (e.g. introduction of non-native species and episodic climatic events; Figure 6). Total fish biomass declined shortly after point-source P control in the late 1970s, followed by gradual establishment of a steady state or even a modest increase until the early 1990s. Evaluation of the effects of reversing eutrophication on fish community composition is confounded by the occurrence of weather extremes, responsible for the catastrophic die-offs of alewife and white perch, whereby yellow perch and walleye gained a competitive advantage. As a result, the fish community rapidly shifted to one dominated by piscivores that effectively controlled pollution-tolerant prey fishes (e.g. alewife, gizzard shad). Our analysis also provided evidence of a distinct decrease in total, planktivore, bentivore, and walleye biomass as well as an increase in sunfish biomass (bluegill, pumpkinseed, black crappie, and largemouth bass) during the recent time period (characterised by a regime shift and the invasion of dreissenids and round goby). Declining walleye abundance can be attributed to reduced ecosystem productivity, decrease in available walleye habitat due to increased water clarity, increased refuges for predators of juvenile walleye due to increased macrophyte cover, and exploitation. Based on the emerging paradigm of catastrophic shifts in nature (Scheffer, Carpenter, Foley, Folke, & Walker, 2001) as well as the insights presented here, the management of stressors that induce slow changes (e.g. nutrient loading, fishing pressure) to the stability of food webs is critical to the maintenance of ecosystem resilience to natural disturbances and other environmental changes (e.g. weather extremes, invasive species). Changes to P2F relationships, as found in our analysis, can be indicative of stressor-induced changes to the energy dynamics of aquatic ecosystems.

ACKNOWLEDGMENTS

Monir Hossain was supported financially by the Great Lakes Action Plan (GLAP) and DFO’s Strategic Program for Ecosystem Research and Advice (SPERA) through a Natural Science and Engineering Research Council of Canada (NSERC) Visiting Fellowship in a Canadian Government Laboratory. Special thanks to Alastair Mathers and Mike Yuille of Ontario Ministry of Natural Resources and Forestry (OMNRF) for providing fish data and helpful comments on the design of our statistical analysis.

FIGURE 6 Structural shifts in the fish community of the Bay of Quinte induced by the combined effects of point-source loading control, extreme climatic events, and introduction of non-native species. The central ongoing management question arises from recent propositions to reduce the targeted total phosphorous (TP) benchmark from 30 μg TP/L to 25 μg TP/L.
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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Hossain, M. Arhonditsis, G. B., Hoyle, J. A., Randall, R. G., Koops, M. A. Nutrient management and structural shifts in fish assemblages: Lessons learned from an area of concern in Lake Ontario. *Freshw Biol.* 2019:64:967–983. https://doi.org/10.1111/fwb.13278
NUTRIENT MANAGEMENT AND STRUCTURAL SHIFTS IN FISH ASSEMBLAGES: LESSONS LEARNED FROM AN AREA OF CONCERN IN LAKE ONTARIO

[SUPPORTING INFORMATION]

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Table 1-SI: Trophic guilds/groups of fish in the Bay of Quinte considered in the present analysis.

| Piscivores               | Planktivores            | Benthivores             | Sunfish                    | Percids/Percoids            |
|--------------------------|-------------------------|-------------------------|----------------------------|----------------------------|
| Largemouth Bass          | Alewife                 | Common Carp             | Bluegill                   | Walleye                    |
| *(Micropterus salmoides)*| *(Alosa pseudoharengus)*| *(Cyprinus carpio)*     | *(Lepomis macrochirus)*    | *(Sander vitreus)*         |
| Walleye                  | Gizzard Shad            | White Sucker            | Pumpkinseed                | Yellow Perch               |
| *(Sander vitreus)*       | *(Dorosoma cepedianum)* | *(Catostomus commersoni)*| *(Lepomis gibbosus)*       | *(Perca flavescens)*       |
| Northern Pike            | Spottail Shiner         | Brown bullhead          | Largemouth Bass            |                            |
| *(Esox lucius)*          | *(Notropis hudsonius)*  | *(Ameiurus nebulosus)*  | *(Micropterus salmoides)*  |                            |
| Bowfin                   |                         |                         | Black Crappie              |                            |
| *(Amia calva)*           |                         |                         | *(Pomoxis nigromaculatus)* |                            |
| Smallmouth Bass          |                         |                         |                            |                            |
| *(Micropterus dolomieu)* |                         |                         |                            |                            |
| Longnose Gar             |                         |                         |                            |                            |
| *(Lepisosteus osseus)*   |                         |                         |                            |                            |
Table 2-SI: Posterior parameters of the multiple regression models developed using chlorophyll $a$, zooplankton, and surface water temperature to predict fish biomass in the Bay of Quinte.

| Group         | Intercept | Slope                      |
|---------------|-----------|----------------------------|
|               |           | Chla | Zooplankton | Surface Water Temperature |
| Mean          |           |      |             |                            |
| All Fish      | 1.01      | 0.80 | 0.25        | 0.01                       |
| Stdev         | 2.11      | 0.23 | 0.24        | 0.09                       |
| Planktivores  | -14.73    | 3.19 | 0.16        | 0.33                       |
| Stdev         | 6.35      | 0.70 | 0.72        | 0.26                       |
| Benthivores   | 3.53      | 0.37 | 0.11        | -0.06                      |
| Stdev         | 1.37      | 0.15 | 0.16        | 0.06                       |
| Piscivores    | -2.70     | 0.67 | 0.63        | 0.06                       |
| Stdev         | 3.29      | 0.36 | 0.37        | 0.14                       |
| Sunfish       | -6.00     | -2.35| 0.87        | 0.35                       |
| Stdev         | 5.07      | 0.59 | 0.60        | 0.22                       |
| Percids       | 0.03      | 0.50 | 0.65        | -0.05                      |
| Stdev         | 3.18      | 0.35 | 0.36        | 0.13                       |
| Walleye       | -1.03     | 0.83 | 0.83        | -0.13                      |
| Stdev         | 4.36      | 0.48 | 0.49        | 0.18                       |
| Yellow Perch  | 1.36      | -0.08| 0.47        | -0.03                      |
| Stdev         | 3.52      | 0.39 | 0.40        | 0.15                       |
| White Perch   | 2.55      | 1.16 | -0.42       | -0.04                      |
| Stdev         | 3.21      | 0.35 | 0.36        | 0.13                       |
| Brown Bullhead| 4.73      | 0.70 | 0.26        | -0.40                      |
| Stdev         | 5.75      | 0.57 | 0.57        | 0.26                       |
| Freshwater Drum| 2.22      | -1.25| 1.41        | -0.21                      |
| Stdev         | 4.20      | 0.46 | 0.48        | 0.17                       |
FIGURES LEGENDS

Figure 1-SI: Trends of the dreissenid wet biomass and standard error per Ekman (mg 0.05 m$^2$+shells) in three different sections (i.e. upper, middle, and lower sections) of the Bay of Quinte.

Figure 2-SI: Posterior average and standard deviation values of the year-specific standardized regression parameters ($\alpha_t$) accounting for the relationship between fish biomass and total phosphorus in three different sections of the Bay of Quinte, Lake Ontario (study period 1972–2013). Dynamic linear modelling analysis based on samples collected with gillnets and trawl nets.

Figure 3-SI: Piecewise regression modelling analysis depicting the actual (black dots) against the predicted (solid line) fish biomass (g per m$^2$ of gillnet) of different groups in the Bay of Quinte. Panels (a-k) correspond to all fish, planktivores, benthivores, piscivores, sunfish, percids, walleye, yellow perch, white perch, brown bullhead, and freshwater drum, respectively.

Figure 4-SI: Year-to-year variability of growing-season (May-October) averages of total phosphorus concentrations (μg L$^{-1}$) in the Bay of Quinte. Panels (a-b) correspond to upper and middle sections, respectively.

Figure 5-SI: Year-to-year variability of growing-season (May-October) averages of zooplankton biomass (mg dry weight m$^{-3}$) in the Bay of Quinte. Panels (a-b) correspond to upper and middle sections, respectively.

Figure 6-SI: Year-to-year variability of growing-season (May-October) averages of the surface water temperature (°C) in the Bay of Quinte. Panels (a-b) correspond to upper and middle sections, respectively.

Figure 7-SI: Year-to-year variability of growing-season (May-October) averages of chlorophyll $a$ concentrations (μg L$^{-1}$) in the Bay of Quinte. Panels (a-b) correspond to upper and middle sections, respectively.
**Figure 1-S1**: Trends of the dreissenid wet biomass and standard error per Ekman (mg 0.05 m$^2$+shells) in three different sections (i.e. upper, middle, and lower sections) of the Bay of Quinte.
Figure 2-SI: Posterior average and standard deviation values of the year-specific standardized regression parameters ($\alpha_t$) accounting for the relationship between fish biomass and total phosphorus in three different sections of the Bay of Quinte, Lake Ontario (study period 1972–2013). Dynamic linear modelling analysis based on samples collected with gillnets and trawl nets.
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Figure 3-SI (Continued)
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Figure 7-SI: Year-to-year variability of growing-season (May-October) averages of chlorophyll $a$ concentrations ($\mu$g L$^{-1}$) in the Bay of Quinte. Panels (a-b) correspond to upper and middle sections, respectively.