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How influential is the role of oligotrophication on the integrity of fish assemblages in the littoral zone?

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ABSTRACT

Food web theory predicts that one of the consequences of oligotrophication is the decline in fisheries following the establishment of nutrient-deficient conditions and low biogenic production. However, emerging evidence suggests that more complex trophic interactions, induced by plankton composition, dietary diversification, temporal and spatial heterogeneity, variations in fish age and size structure can lead to ecosystem responses that deviate from theoretical predictions; especially in the shallow littoral zone. In this study, two *end-to-end* modelling strategies are used to characterize potential food web structural shifts and overall ecosystem productivity in response to oligotrophication. Our modelling strategy draws upon empirical and theoretical evidence from the Bay of Quinte, a semi-enclosed embayment in northeastern Lake Ontario that has been subjected to phosphorus (P) abatement strategies in the 1970s. We first show that the role of food abundance has been a primary factor shaping fish production, but the fish community gradually responded to the reduced availability of pelagic staples of their diet by displaying greater reliance upon alternative sources, including benthic and other autochthonous (or even allochthonous) food items. Our analysis further suggests that degree of diet overlap between competing trophic guilds can significantly modulate realized biomass levels. The composition of the autotrophic community is another major confounding factor that can induce significant variations from the predicted food web productivity patterns in response to oligotrophication. Overall, our analysis suggests that the proposed reduction of the ambient total phosphorus levels may not necessarily trigger a significant decline in fish biomass in the Bay of Quinte.

Introduction

Resource availability is considered the primary driver of ecosystem productivity. The variability in resource subsidies that a system receives from the surrounding environment can modulate the production of the autotrophs, which can then shape the productivity of higher trophic levels. Aquatic environments characterized by nutrient deficiency and low productivity are classified as oligotrophic, and the process towards the prevalence of such conditions is known as oligotrophication (Naumann, 1929). Structural and functional ecosystem shifts triggered by the transition to oligotrophication are often perceived as favorable relative to conditions experienced in formerly eutrophic environments, such as the decrease of pelagic primary productivity (Phillips et al., 2005; Jeppesen et al., 2005; Signorini et al., 2015), increased taxonomic richness and diversity (Özkan et al., 2016; Murphy et al., 2018), and improved water clarity, owing to reduced suspended particles, which in turn often leads to a resurgence of macrophytes (Murphy et al., 2018). Nevertheless, there are growing concerns in the literature that when the productivity falls below a minimum level under protracted conditions of oligotrophication, the broader ecosystem services may be compromised (Dove, 2009; Hossain et al., 2019). A synthesis of long-term monitoring studies from Danish and other European lakes (Jeppesen et al., 2005; Gerdeaux et al., 2006) lends support to this notion, as the reduced primary productivity can translate into a discernible decline in the flow of energy along the food web (Randall et al., 1995; DeBruyn

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et al., 2003), often manifested as zooplankton biomass reduction (Gaedke and Wickham, 2004; Phillips et al., 2005) and distinct decrease in fish recruitment and production (Gerdeaux et al., 2006; Lorenz et al., 2019).

The underlying mechanisms of oligotrophication are often convoluted with a multitude of physical and chemical factors that can collectively exacerbate or moderate the impact of reduced resource supply on food-web productivity. The hydrodynamic transport of nutrients within an aquatic system is a case in point, having the capacity to modulate the broader ecosystem productivity. For example, the seasonal circulation patterns of the northern Adriatic Sea are responsible for spreading nutrient-rich water masses from the river plumes, thereby contributing to an increase in winter anchovy catches following an increase of the main staples of their diet (e.g., ciliates), despite the prevailing oligotrophication in the region (Kraus et al., 2015). In stark contrast, the establishment of a more intense thermal stratification in the open-ocean subtropical gyre can limit resource replenishment in the oceanic mixed layer due to reduced diffusive vertical exchange (Sarmiento et al., 2004), further expanding the areas of low primary productivity over recent decades (Irwin and Oliver, 2009).

The effects of a gradual decline in resource availability can be similarly altered by biological stressors, such as the invasion of exotic species, often inducing a suite of changes in individual trophic levels and the broader food web alike. A characteristic example is the invasive dreissenid mussels that have increased P retention by the benthic community in the littoral zone and presumably accelerated the oligotrophication processes in the pelagic environment (Vanderploeg et al., 2002; Hecky et al., 2004). The establishment of dreissenids in the Great Lakes during the mid-1990s triggered ecological shifts similar to oligotrophication with significant reduction of phytoplankton abundance (Higgins and Vander Zaden, 2010) and zooplankton productivity (Johannsson et al., 2000). The dreissenid mussels also altered the benthic community structure by replacing native bivalves, e.g., *Sphaerium* spp (Mills et al., 2003), and mediating the proliferation of amphipods and oligochaetes presumably due to the microenvironment created by dreissenid excreta (Dermott et al., 1998; Haynes et al., 1999). Nonetheless, the subsequent invasion of round goby (*Neogobius melanostomus*) led to the establishment of new trophic pathways that moderated the impact of oligotrophication through the consumption of dreissenids and return of the benthic energy production to the upper food web (Truemper and Lauer, 2005; Johnson et al., 2005; Campbell et al., 2009). Analysis of stomach contents of piscivorous fish, such as walleye (*Sander vitreus*) and white bass (*Morone chrysops*), revealed their increasing reliance on round goby relative to other pelagic food sources (Johnson et al., 2005). Alongside the shifts in trophic pathways induced by invasive species, empirical evidence from the Great Lakes suggests that the impact of oligotrophication on ecosystem productivity can also be modulated by the dynamics of major prey species, such as the decline of *Diporeia*, (Madenjian et al., 2006; Bunnell et al., 2009), severe weather conditions (Hurley, 1986; Hossain et al., 2019), selective control of exotic prey fish, such as alewife (*Alosa pseudoharengus*) and sea lamprey (*Petromyzon marinus*) (Mills et al., 2003), and stocking of lake trout (*Salvelinus namaycush*) and rainbow trout (*Oncorhynchus mykiss*) that are valuable for recreational fishing (Mills et al., 2003).

Bay of Quinte is a shallow embayment located at the northwestern end of Lake Ontario. Like most of the Great Lakes, it is a typical example of a freshwater system that has been subjected to oligotrophication following the implementation of P abatement strategies in the 1970s (Minns et al., 1986; Nicholls and Carney, 2011; Arhonditsis et al., 2016). Besides the typical patterns, i.e., lower ambient total phosphorus (TP) levels leading to reduced primary productivity and ultimately decline of total fish biomass, there is empirical evidence of a distinct compositional shift in the fish assemblage in the Bay of Quinte, whereby the historically dominant planktivorous fish (∼60%) were replaced by piscivores (∼40%) shortly after P control. Even more so, the likelihood of an additional ambient TP decline is predicted to induce a greater than 20% reduction in total fish biomass, and further composition shifts with the biomass of planktivores and walleye projected to decrease by more than 60% and 30%, respectively (Hossain et al., 2019). While the aforementioned transition to piscivory is an expected pattern often attributed to oligotrophication (Jeppesen et al., 2005), the gradual prevalence of benthivorous fish (>60%) suggest that the fish community response may be regulated by more complex ecological mechanisms in this semi-enclosed embayment (Hossain et al., 2019). Productivity in the heterogeneous littoral habitat of the Bay of Quinte may be more resilient to the dynamics of autochthonous food sources than the offshore waters in Lake Ontario, due to behavioural and life cycle adaptations of critical prey fish species (Sabel et al., 2020), potential subsidies of allochthonous organic input from tributaries of the surrounding watershed (Vadeboncoeur et al., 2002), and alternative energy pathways generated by benthic invasive organisms, such as dreissenids and round goby (Campbell et al., 2009; Fera et al., 2017). Thus, it can be argued that the adoption of the traditional linear food-chain paradigm to draw inference about the ecosystem productivity may be obsolete, as it downplays the complexity of trophic interactions, as well as the potential of species behavioral adaptation under new environmental conditions generated by anthropogenic actions (e.g., management plans) or major ecological events (e.g., invasive species) (Latour et al., 2003).

Striving for an effective balance between water quality and fisheries management, the present study examines the importance of a suite of factors to modulate the impact of oligotrophication on the integrity of fisheries in the littoral zone, including the capacity of the autotrophic community composition to regulate the flow of energy through the food web, the potential of allochthonous matter and/or increased reliance upon benthic food sources to compensate for the gradual decline of pelagic biogenic production, and the ability of diet adaptation to shape the productivity of competing trophic guilds of fish. To address this objective, we developed two complementary *end-to-end* modelling strategies, a Bayesian hierarchical structural equation model and a process-based food-web model, to characterize potential alterations in the trophodynamics and overall ecosystem productivity in response to oligotrophication in littoral environments. The first model offers a multivariate statistical (data-driven) strategy to examine the relative strength of the trophic pathways among key biotic compartments of the Bay of Quinte food web, i.e., phytoplankton, zooplankton, and three fish trophic guilds (planktivores, benthivores, piscivores), as evolved over time from the external nutrient loading control and disturbances induced by invasive species (dreissenid mussels, round goby). The mechanistic foundation of the second model allows addressing more granular topics associated with the role of plankton composition and dietary diversification of fish on the broader ecosystem productivity. Our hypothesis is that the littoral environment offers a multitude of alternative ecological pathways that can modulate the risk of a severe decline in fish productivity following the gradual prevalence of oligotrophic conditions. Specifically, we hypothesize that the abundance of benthic and other autochthonous (or even allochthonous) food items allows species with facultative generalist feeding behaviour at different life stages -walleye, yellow perch (*Perca flavescens*), white perch (*Morone americana*), brown bullhead (*Ameiurus nebulosus*), white sucker (*Catostomus commersoni*)- to adapt to the non-stationary changes of the pelagic environment and realize positive net growth rates. Using this combination of empirical and theoretical modelling, our study examines whether a dramatic collapse of fisheries is a likely scenario that could emerge from the continuing nutrient loading control in the Bay of Quinte, as well as other sites in the nearshore zone of the Great Lakes and elsewhere.

Methods

Bayesian hierarchical structural equation modelling

We used two modelling strategies to examine the effects of oligotrophication on food-web dynamics in the Bay of Quinte, while parsing out the potential shifts of the fish community triggered by the dreissenid invasion. The first approach, structural equation modelling (SEM), is a multivariate statistical method that encompasses both factor and path analysis (Fig. 1a,b), whereby a network of relationships can be evaluated by dissecting intertwined ecological pathways into a series of direct and indirect relationships (Bollen, 1989). Counter to multivariate regression models, SEM allows examining the indirect effects between two variables by accounting for the effects of other intermediary variables (Arhonditsis et al., 2006; Kenney et al., 2009). In this "a priori" statistical method, the starting model is a hypothesized ecological structure that reflects our best understanding of ecosystem mechanisms, testable hypotheses, and/or research questions. The formulation of this starting model postulates an expected covariance structure, which is tested against the covariance matrix from observed data, and the associated SEM parameters are then estimated by fitting methods such as maximum likelihood, unweighted least squares, and generalized least squares (Bollen, 1989).

In the present study, we developed a Bayesian hierarchical SEM approach that has several distinguishing advantages over the classical method. The available data were pooled from two locations, Belleville and Hay Bay, and two time stanzas, before (1975–1994) and after (1995–2013) the dreissenid invasion, to account for the spatial heterogeneity and the major ecosystem disturbance occurred in the Bay of Quinte during the study period (Fig. 2 and Electronic Supplementary Material (ESM) Fig. S1). Consequently, the parameter estimation is based on a hierarchical configuration,

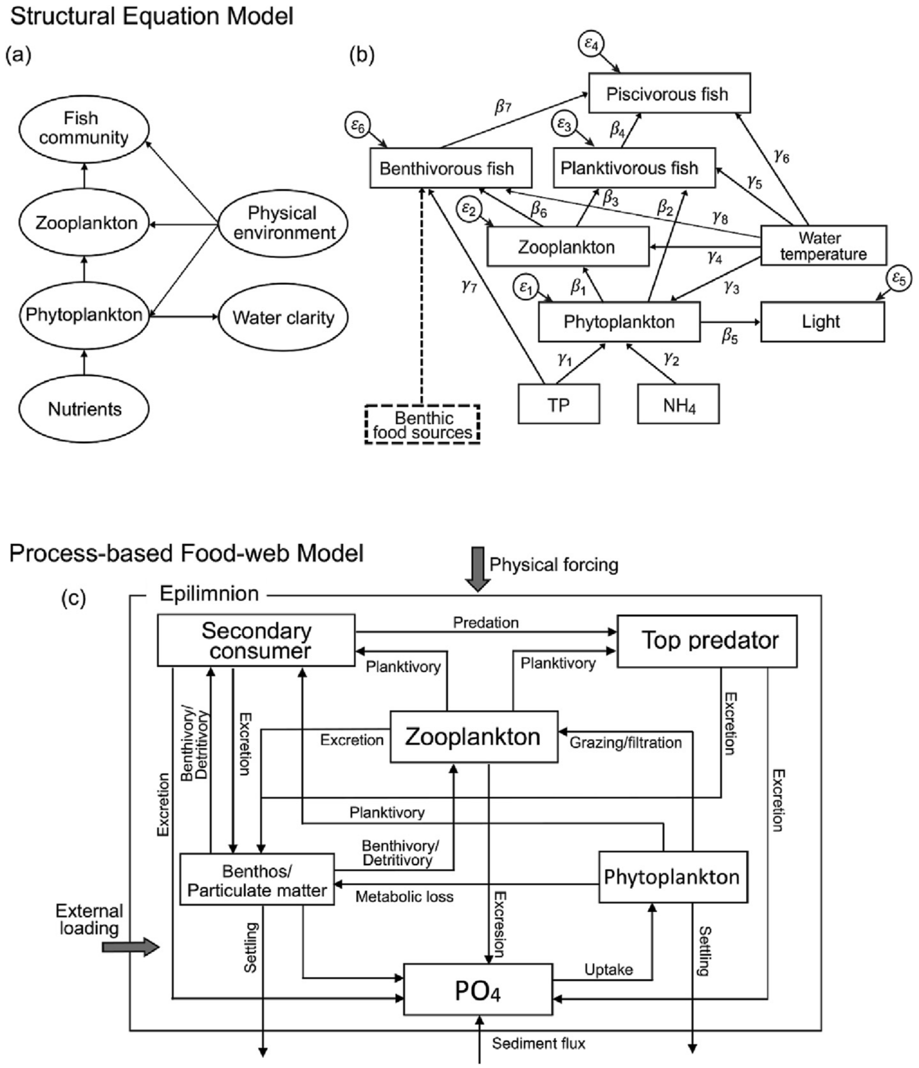

Fig. 1. Ensemble modelling strategy used in this study. Bayesian hierarchical structural equation model (SEM) based on (*a*) a generic conceptualization of the regulatory role of abiotic conditions (nutrients, water temperature, light environment) on the trophic relationships among phytoplankton, zooplankton, and fish community. (*b*) The actual SEM developed for the Bay of Quinte to characterize the dominant ecological pathways among phytoplankton, zooplankton, planktivorous, benthivorous, and piscivorous fish. The dotted box and arrow represent the pathway between benthivorous fish and benthic food sources that were not included in the present analysis. Process-based food-web model (*c*) to reproduce the trophodynamics among a primary producer, primary consumer, secondary consumer, and top predator.

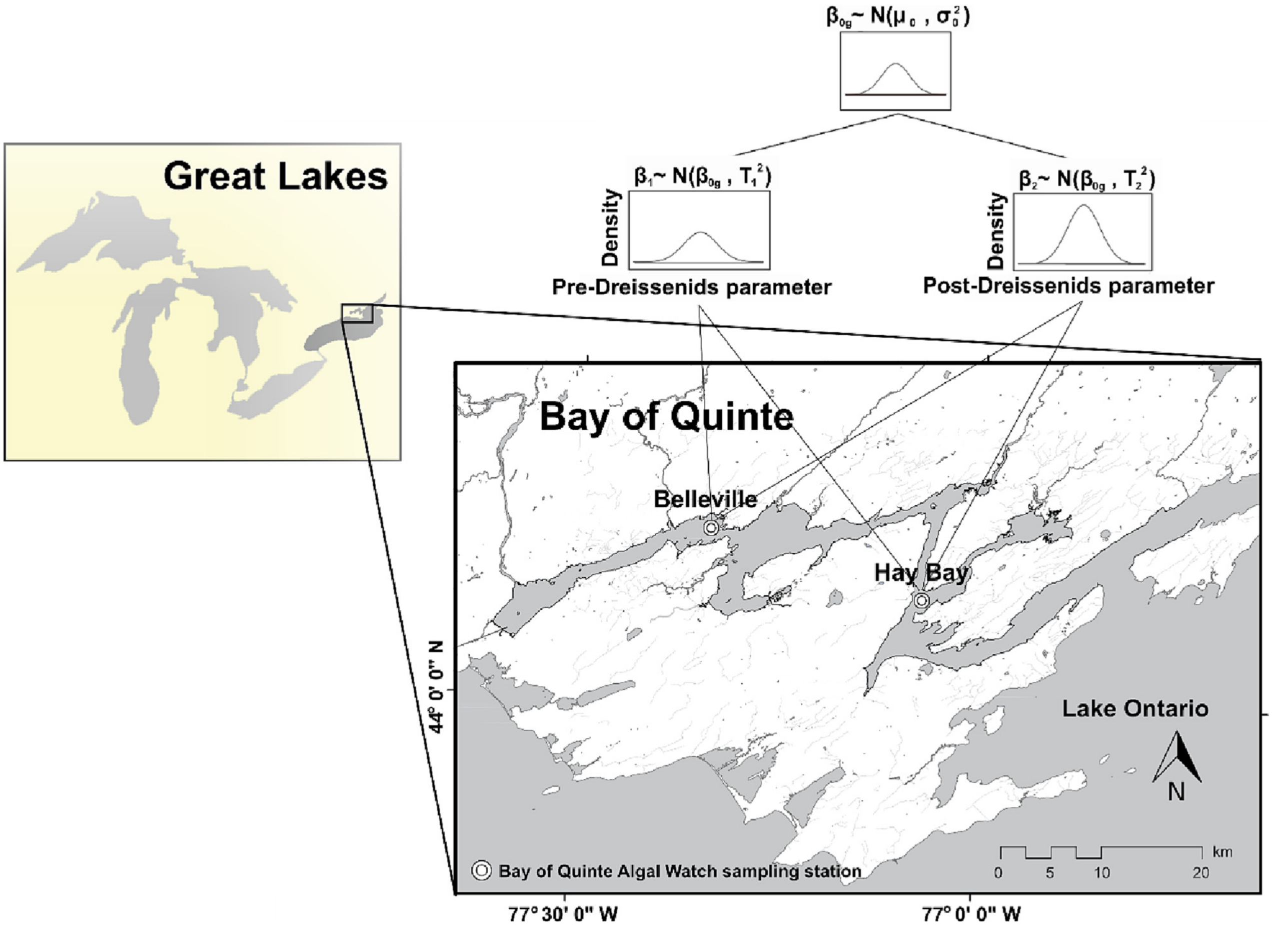

Fig. 2. Map of the Bay of Quinte and two sampling locations (Belleville and Hay Bay) used for the Bayesian hierarchical structural equation model. The hierarchical levels represent (*i*) the global parameters (hyperparameters) that collectively characterize the ecological pathways over the two locations of the Bay throughout the study period, and (*ii*) the parameters associated with the time stanzas before and after the invasion of dreissenid mussels.

whereby the likelihood of distinct structural shifts induced by the invasion of dreissenids is explicitly examined at the first level, while the common characteristics across the two sampling sites (Belleville and Hay Bay) of the modelled system are captured by the hyper-parameters at the top level. The use of Bayesian inference is particularly suitable for the present study, as the use of averaged data over the growing season per year (see ESM Section D Data Description) decreased the sample size (i.e., n = 19 and 18 for the pre- and post-dreissenids period, respectively), and thus the classical parameter estimation methods are not robust (Congdon et al., 2003). Because the Bayesian approach does not rely on asymptotic theory and Markov Chain Monte Carlo (MCMC) samples are taken directly from the model posterior, any problems of multimodality or non-Gaussian likelihood surfaces stemming from small sample sizes can be effectively addressed (Congdon et al., 2003). An additional advantage of the Bayesian approach is that it allows the explicit consideration of various sources of uncertainty (measurement error, parametric uncertainty), and therefore the predictive statements drawn from the model convey significantly more information than point estimates in regards to the true knowledge we possess about the studied system (Arhonditsis et al., 2006; 2007a).

The structural equation model for the Bay of Quinte depicts the linkages between the lower food web -revolving around the interplay among nutrients, phytoplankton, and zooplankton- with three trophic guilds of fish, defined on the basis of their feeding strategies typically reported in the literature (ESM Table S1). Following our earlier work (Arhonditsis et al., 2006), we first conducted exploratory analysis to identify the optimal model structure, given the available data and hypothesized conceptual food-web structure (Fig. 1a). Using a suite of statistical criteria, i.e., posterior *p*-value, Deviance Information Criterion, and path identifiability (Congdon et al., 2003), we examined a number of alternative structural equation models and identified the most parsimonious one for the subsequent hierarchical analysis (Fig. 1b). We used growing-season (May–October) averages for all the variables included in the final SEM. Among the available dissolved and particulate nutrient forms, TP and NH_4 were selected as the best surrogate variables of the trophic status. Water temperature was used as the physical factor that shapes the metabolic activities of the biotic compartments, while the model also considers the impact of phytoplankton standing biomass on underwater light attenuation. Planktivorous fish (alewife, gizzard shad, spottail shiner) was designed to be a secondary consumer that feeds upon both zooplankton and phytoplankton, whereas piscivorous fish (walleye, largemouth bass, northern pike, bowfin) was specified as a tertiary consumer that preys upon the other two fish groups (planktivores and benthivores). Benthivorous fish (white sucker, yellow perch, white perch, brown bullhead, common carp) was specified to feed on zooplankton as well as on benthos/particulate matter (either biogenic or of terrestrial origin). The main caveat of the latter specification is the lack of consistent benthic abundance data during the study period, which did not allow direct evaluation of their relationship with the fish assemblage. To overcome this problem, we used TP as a proxy assuming that it displays a positive relationship with the abundance of the benthic community.

Notwithstanding the fact that TP is not orthogonal to phytoplankton, it does provide a surrogate variable to examine a food-web configuration that deviates from the usual linear approaches, such as "phytoplankton-zooplankton-planktivorous fish-piscivorous fish". This simplification provided the motivation for the development of a complementary mechanistic model to present a more granular examination of the trophodynamics that may be manifested in response to oligotrophication (see following section).

Existing evidence suggests that dreissenid mussels have induced structural shifts in the phytoplankton community of the Bay of Quinte, gradually decreasing N_2-fixing species (*Aphanizomenon* spp. and *Anabaena* spp.) and increasing the frequency of outbreaks of toxin-producing *Microcystis* spp. (Shimoda et al., 2016; Kelly et al., 2019). These structural shifts of the phytoplankton community may have broad implications for the diets of the primary consumers, and ultimately influence the productivity of fish populations (Bowen and Johannsson, 2011). Morphological characteristics, toxicity, and lower nutritional value of cyanobacteria (Müller-Navarra et al., 2000), such as *Microcystis* spp. have been suggested to represent an inferior food source for zooplankton growth (von Elert et al., 2003), which may have influenced the efficiency of energy transfer through the food web. Based on the differences between the pre- and post-invasion pathways, the hierarchical SEM configuration will allow assessing the potential shifts in the reliance of primary and secondary consumers on autochthonous and allochthonous sources before and after the invasion of dreissenids, and subsequently examine the implications for their trophic linkages with piscivorous fish. A brief description of the Bayesian SEM formulation, the computational aspects of this modelling exercise, and the data used are provided in ESM Sections B and D.

Process-based Food-web modelling

The second approach, a process-based food-web model was used to elucidate facets of ecosystem functioning that can not be captured by the Bayesian hierarchical SEM (Fig. 1c). This simple mechanistic food-web model was built upon the classical Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) modelling construct designed to reproduce the dynamics of aquatic lower food webs using the limiting nutrient as the currency (Arhonditsis et al., 2007b). We introduced two fish groups to account for the capacity of feeding and metabolic activities of the secondary consumer (F_{CS}) and top predator (F_{PR}) to modulate the planktonic food-web dynamics and overall system response to oligotrophication. The detailed design of our food-web model ($NPZDF_{CS}F_{PR}$), along with the parameter ranges used are provided in ESM Section C of (Table SC1), while the data used for model calibration are described with references in ESM Section D. Here, we briefly describe the general structure and key aspects of our model that are the most relevant for the objectives of the present study.

Consistent with traditional plankton models, $NPZDF_{CS}F_{PR}$ includes the lower food-web state variables: dissolved inorganic phosphorus (PO_4, $\mu g\ P\ L^{-1}$), phytoplankton ($\mu g\ C\ L^{-1}$), and zooplankton ($\mu g\ C\ L^{-1}$). In order to characterize alternative food sources for the fish community, the typically considered detrital phosphorus in NPZD models was redefined as an aggregated variable of benthos and particulate material (both allochthonous and autochthonous) ($\mu g\ P\ L^{-1}$). The growth of autotrophic community via PO_4 uptake is transferred to the primary consumer (zooplankton) by grazing. The added two fish groups ($\mu g\ C\ L^{-1}$) differ with respect to their feeding strategies with parameters that reflect their preference on food sources. One of the two generic fish assemblages represented the top-predator (F_{PR}), feeding on the other fish group and zooplankton, whereas the second fish group was assumed to be an omnivorous secondary consumer (F_{CS}), feeding on phytoplankton, zooplankton, and other particulate food items. Their feeding capacity on each food source is regulated by the corresponding food preference parameters, and thus the secondary consumer can emulate the role of either benthivorous or planktivorous fish included in the SEM approach, depending on the food preference vectors assigned. Because of the wide range of diets assigned to the two fish compartments, as expressed by the different fractional contributions of phytoplankton, zooplankton, and particulate matter to the diet of the secondary consumer, or zooplankton, particulate matter, and secondary consumer to the diet of the top fish predator, our study treats the prey-predator relationships as a continuum.

The relative availability of each food source was also postulated to be another covariate of food selectivity to avoid the potential starvation of the fish populations. The representation of the benthos/particulate material of our $NPZDF_{CS}F_{PR}$ model is another critical feature to complement our SEM approach. Although our SEM explicitly considers a (log–log linear) pathway between TP and the biomass of the secondary consumer (benthivores), the inclusion of TP merely served as a proxy of the trophic status of the system which in turn was assumed to be positively related to the benthic food availability. Thus, the differential equation of the mechanistic model not only accounts for the metabolic sources (death, excretion) and sinks (bacteria-mediated mineralization, consumption by zooplankton and secondary consumer fish) of the simulated biota, but also considers potential biomass of the benthic biota and an external (terrestrial) input that replenishes the particulate pool with potentially edible material. In doing so, it aims to recreate the potential implications of a gradual shift to benthification for the integrity and sustainability of fisheries.

We examined thirty-six (36) parameter combinations that reflect a multitude of feeding strategies of two fish groups and zooplankton in order to reproduce the range of potential food web responses to oligotrophication. Specifically, zooplankton are assumed to graze upon phytoplankton and benthos/particulate material, and thus our modelling experiments varied their feeding strategy from herbivory, filter feeding (equal preference for the two food sources), to a particulate material-dominated diet. Feeding rates for both top-predator and secondary consumer were specified to follow a type II functional response, whereby the rate increases with prey density up to an intrinsic maximum capacity. Selectivity strategies for the secondary consumer fish groups varied from a zooplankton-dominated diet to a greater reliance on benthic food sources, while phytoplankton was the third staple of their diet and accounted for a constant 20% of their preferential feeding. Likewise, the parameter used as a proxy for food preference of a given trophic guild recreated scenarios of a top predator gravitating towards zooplanktivory (young-of the-year fish) or towards planktivorous fish (adult fish) and accordingly examine their impact on food-web stability. The food-preference scenarios closely reproduced the dietary patterns of the dominant fish species in the Bay of Quinte, as derived by empirical evidence reported by Bowlby and Hoyle (2011), Hoyle et al. (2012; see their Table 2), and Hoyle et al. (2017). In summary, the basic premise of our analysis is the development of a "virtual environment" that can offer the flexibility to represent the potential adaptation (i.e., foraging activities and metabolic rates) of biotic assemblages and examine ecosystem resilience to external forcing variations, such as reduced nutrient loading, and the likelihood of occurrence of regime shifts. Feeding strategy scenarios and associated parameter values are provided in the Supporting Information (ESM Fig. S2 and Table SC1).

Nutrient management and invasive species (dreissenid mussels, round goby) have induced distinct structural shifts in the phytoplankton community of the Bay of Quinte (Nicholls and Carney, 2011; Shimoda et al., 2016). We thus designed a second set of experiments aiming to emulate compositional phytoplankton shifts from r-strategists (or an algal assemblage dominated by diatom-like species with fast growth and metabolic rates, superior phosphorus kinetics, and higher settling rates) to K-strategists (or cyanobacteria-like species), and understand their potential effects on fish productivity (Table SC1). Food palatability and nutritional values (assimilation efficiency) along with the differential preferences from the primary and secondary consumers were also considered for each phytoplankton scenario. For example, the maximum growth efficiency of zooplankton and secondary consumer via phytoplankton ingestion has an upper bound of 25% of ingested mass, when phytoplankton was specified as a K-strategist, considered to be of poor-food quality for consumers, whereas a maximum of 65% of the high food-quality diatoms was stipulated to support the growth of herbivorous zooplankton and planktivorous fish. A third characterization of the phytoplankton community, referred to as "default", aimed to depict the continuum between diatom- and cyanobacteria-dominated assemblages that are closer to the current state of the Bay of Quinte. The series of experiments were repeated under different trophic conditions (oligotrophic, present, and eutrophic) to investigate the degree that ambient nutrient levels and phytoplankton community composition shape the trophodynamics and subsequent fish productivity.

Results

The Bayesian hierarchical SEM provided a satisfactory fit to the observed data for all modelled variables, expected from the benthivorous fish biomass and underwater light attenuation in Hay Bay (ESM Table S2 and Fig. S3). While there were no drastic shifts in the relative strength of the individual ecological paths between the two study periods, our SEM confirmed the central role of the autotrophic community in the Bay of Quinte food web (Fig. 3, Table 1 and ESM Tables S3-S4). The path coefficients associated with phytoplankton, such as TP to phytoplankton (γ_1), phytoplankton to zooplankton (β_1), and phytoplankton to planktivores (β_2) were consistently high (>0.500) relative to other pathways during both pre- and post-dreissenid periods. We also highlight the distinct signature of NH_4 to phytoplankton (γ_2), which reinforces empirical evidence that nitrogen availability is a co-limiting factor that shapes primary productivity in the system. In stark contrast, the paths associated with the primary consumer (zooplankton) were weak and poorly identified. The mean values of the predictive distributions of the coefficients that link zooplankton with fish community, i.e., zooplankton to planktivores (β_3) and zooplankton to benthivores (β_6), were lower than 0.100 and further shifted to negative in the post-dreissenid period. It should also be noted that the path coefficients associated with zooplanktivory were poorly identified with high coefficients of variation of 150–350% (Table 1 and ESM Fig. S4), indicating that the nature and strength of the trophic relationships between zooplankton and fish in the Bay of Quinte have not been registered with the available data. One of the most discernable changes between the two time periods was the linkage from TP towards the top-predator via benthivorous fish. The relative strength of the path between TP and benthivores (γ_7) increased from 0.264 to 0.437, whereas the path between benthivores and piscivores (β_7) decreased from 0.884 to 0.624. Nevertheless, the latter linkage (benthivores to piscivores) remained strong during the post-dreissenid period compared to the alternative path from planktivores to piscivores (β_4), which was suggestive of a weak and poorly identified relationship, consistently falling below 0.100. With respect to the physical environment (ESM Fig. S5), our SEM analysis revealed a strong negative relationship between standing phytoplankton biomass and underwater light attenuation ($|\beta_5| > 0.700$). The other notable finding was the consistently weak and poorly identified signature of water temperature on the abundance levels of the biotic compartments considered, which may be evidence that teasing out the role of temperature requires finer granularity with respect to the temporal scale and taxonomic resolution considered (see also following discussion).

Based on the characterization of the major pathways underlying the Bay of Quinte food web, we examined the potential impact of oligotrophication on the biomass of the fish guilds considered. A recent study by Hossain et al. (2019) (see their Fig. 5 and Table 3) predicted that an average TP decrease from 30 to 25 μg L^{-1} in the Bay of Quinte will reduce by approximately 20% the median total fish biomass, and by more than 65% and 20% the biomass levels of planktivores and piscivores, respectively. However, Hossain et al.'s (2019) predictions were based on a simpler multiple regression model that directly linked the response of fish biomass to the ambient TP variability, while keeping the other two covariates (zooplankton biomass and surface water temperature) at their average levels during the post-dreissenid era. Our SEM similarly predicted that a 20% reduction of the average TP concentration triggered a significant decline in the planktivorous fish biomass levels, which dropped by 45% in response to a nearly 25% decrease of the total phytoplankton (Table 2). Nonetheless, the most notable difference from the earlier study was our SEM predictions related to benthivorous and piscivorous fish, which were suggestive of a remarkable resilience to the scenario of lower availability of their autochthonous food items. Rather than connecting their biomass levels directly with the ambient TP variability, SEM explicitly considered alternative trophic pathways that can conceivably modulate the functional integrity of fish populations to variations of their food sources, which apparently moderated earlier predictions regarding the future of fisheries in the Bay of Quinte.

The introduction of a process-based food-web model offered a complementary tool to examine the potential role of two major factors that could shape the predicted response of fisheries to nutrient loading reduction; namely, the diet overlap between coexisting trophic guilds of fish, and the predominant features (growth and metabolic strategies, nutritional quality as a staple of the diet of food web consumers) of the algal assemblage. We first conducted modelling experiments that highlighted the regulatory role of the degree of diet overlap between competing trophic guilds on their productivity (Fig. 4). When the secondary consumer and top-predator fish competed for the same food source (zooplanktivory, Fig. 4b, strategy 1), the biomass of the top-predator was consistently low regardless of the trophic conditions simulated (Fig. 4a-c). To the contrary, when the two fish groups displayed minimal diet overlap, i.e., diet dominated by benthos/particulate material food sources for the secondary consumer and piscivory for the top-predator (Fig. 4b, strategy 5), the top-predator biomass was consistently high even when an oligotrophic environment was recreated (∼1,500 μg C L^{-1}, Fig. 4c). Nonetheless, the benefits from a distinctly different feeding strategy to the productivity of the top-predator biomass were not realized evenly across all the scenarios examined within a given trophic environment. Namely, the top-predator reached higher biomass levels when the secondary consumer mainly feeds upon benthic/particulate material food sources (Fig. 4b, strategy A), whereas a predominantly piscivorous top predator could not sustain an equally high biomass when the secondary consumer is characterized by zooplankton-dominated diet (Fig. 4b, strategy B). Interestingly, a benthic feeding secondary consumer cannot always sustain fisheries within oligotrophic environments, even if piscivory is the main feeding strategy for the apex predator, which is suggestive of a lack of sufficient energy to fuel the aquatic food web (Fig. 4c). According to our modelling experiments, the secondary consumer displayed more static behaviour

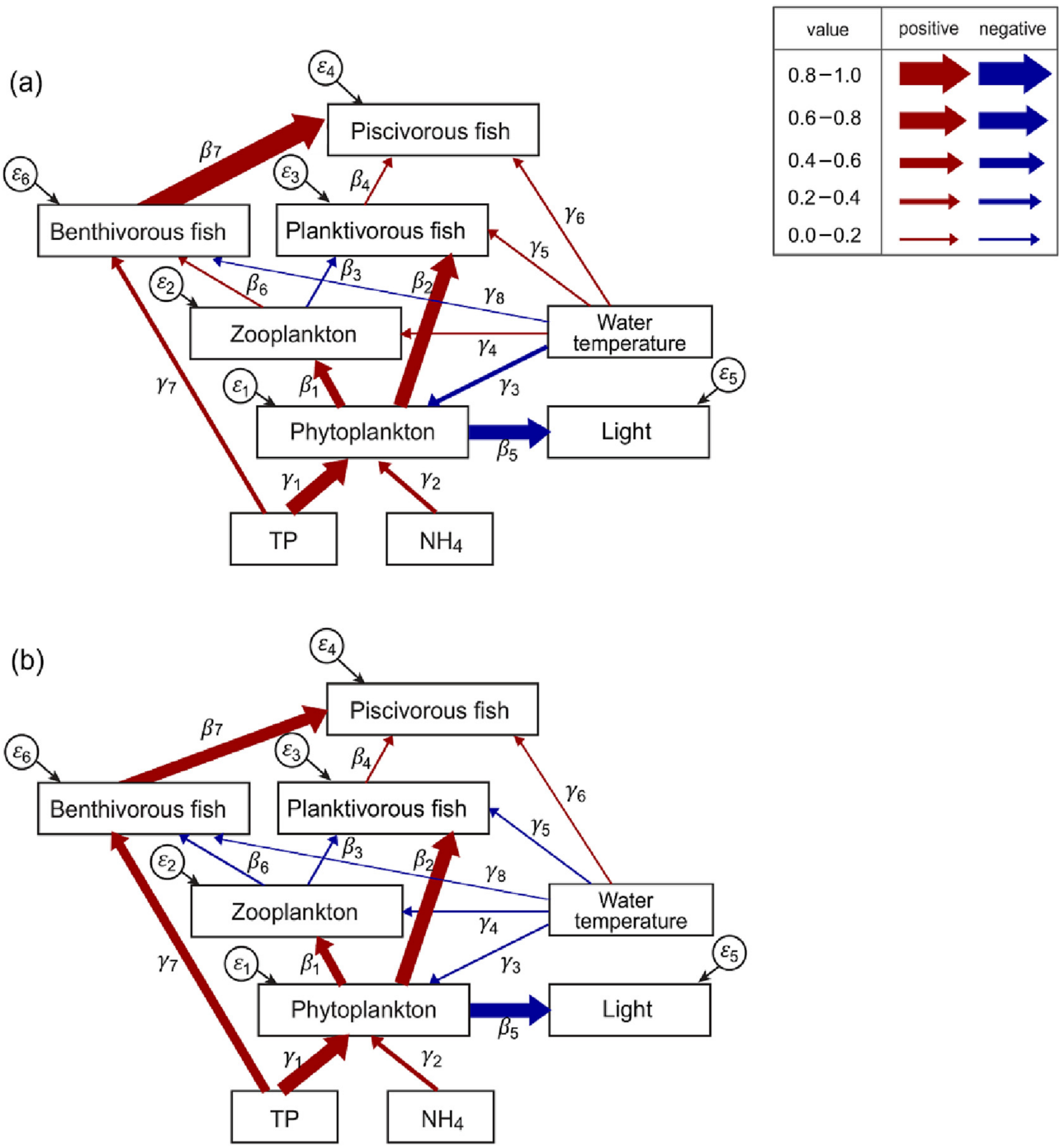

Fig. 3. Characterization of the Bay of Quinte food web, as derived from the Bayesian hierarchical SEM, for the (a) pre- and (b) post-dreissenid invasion periods. The thickness of each arrow denotes the relative strength of the pathway between two variables, which in turn is determined by the mean value of the corresponding standardized path coefficient (see Table 1) and a 5-level categorization. Color of each arrows represents the sign (red: positive, blue: negative) of the pathway. TP concentrations in the upper segment of the Bay of Quinte declined from 43.9 ± 16.5 μg TP L^{-1} during the post-P control/pre-dreissenid invasion period to 33.8 ± 14.7 μg TP L^{-1} during the post-dreissenid invasion period (Shimoda et al., 2016). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with higher biomass levels registered when they opted for intense zooplanktivory and the top predator biomass lay at the lowest values (Fig. 4d-f).

Our analysis subsequently examined the potential of structural shifts in the phytoplankton assemblage to induce variations in the predicted food web productivity patterns, based on the fish community feeding strategies (Fig. 5 and ESM Fig. S6). When the primary producers are predominantly r-strategists (fast growth and metabolic rates, superior nutritional food quality), the degree of diet overlap among the coexisting fish groups does not play a significant role on the productivity of the upper trophic level, resulting in consistently low and high levels of biomass for top predator and secondary consumer, respectively (Fig. 5a,b). In stark contrast, the productivity of the top fish predator and secondary consumer display a distinctly wider range when K-strategists (slow growth and metabolic rates, inferior nutritional food quality) dominate the algal assemblage, and consequently the feeding strategies of fish emerge as an important regulatory factor. In fact, the biomass of the top predator could display a two-fold increase when minimal diet overlap is postulated for the two trophic guilds of the fish assemblage (strategy 5; piscivorous top predator and benthic feeding secondary consumer) relative to the productivity projected under strong resource competition (strategy 1; zooplanktivory by both top predator and secondary consumer). Another critical aspect of this second modelling experiment is that the prevalence of high algal food quality, and the consequent improvement in the flow of energy through the food web primarily benefits the second consumer, displaying its highest biomass levels across the different food web configurations examined (Fig. 5b; see also additional results in ESM Fig. S7). In our virtual environment, the trajectory of the top predator follows closely those of zooplankton (Fig. 5c) and phytoplankton (Fig. 5d), which suggests that food quantity (and not just quality) is a major driver of overall food web productivity. However, it is important to note that the scenario of an algal

Table 1
Bay of Quinte SEM standardized posterior path coefficients. p($\theta > 0$) indicate the probability of each path being positive. Probability values greater than 90% suggest that the odds of a positive path are very high (slope is likely positive), values lower than 10% suggest that the odds of a positive path are very low (slope is likely negative), values between 10% and 90% suggest the posterior evidence is inconclusive.

Structural Equation Model		Pre-dreissenid			Post-dreissenid		
Path	Symbol	Mean	SD	p($\theta > 0$)	Mean	SD	p($\theta > 0$)
Phytoplankton ← *TP*	γ_1	0.639	0.095	>99.9%	0.715	0.122	>99.9%
Phytoplankton ← NH_4	γ_2	0.320	0.097	>99.9%	0.228	0.118	97.3%
Phytoplankton ← Temperature	γ_3	−0.218	0.093	1.0%	−0.125	0.115	13.9%
Zooplankton ← Temperature	γ_4	0.054	0.125	66.7%	−0.092	0.156	27.8%
Benthivores ← Temperature	γ_8	−0.055	0.133	34.0%	−0.049	0.156	37.7%
Planktivores ← Temperature	γ_5	0.173	0.113	93.7%	−0.018	0.146	45.1%
Piscivores ← Temperature	γ_6	0.120	0.092	90.4%	0.024	0.113	58.4%
Secchi depth ← Phytoplankton	β_5	−0.715	0.104	<0.01%	−0.704	0.103	<0.01%
Zooplankton ← Phytoplankton	β_1	0.418	0.135	>99.9%	0.504	0.135	>99.9%
Benthivores ← *TP*	γ_7	0.264	0.145	96.6%	0.437	0.185	99.1%
Benthivores ← Zooplankton	β_6	0.041	0.149	60.8%	−0.116	0.170	24.8%
Planktivores ← Phytoplankton	β_2	0.659	0.119	>99.9%	0.673	0.125	>99.9%
Planktivores ← Zooplankton	β_3	−0.034	0.117	38.6%	−0.054	0.129	33.8%
Piscivores ← Benthivores	β_7	0.884	0.130	>99.9%	0.624	0.107	>99.9%
Piscivores ← Planktivores	β_4	0.041	0.092	67.2%	0.086	0.114	77.5%

Table 2
Prediction of average changes in biomass of the biotic compartments considered by the Bayesian hierarchical SEM under a 20% TP loading reduction scenario.

Variables	30 (TP µg L^{-1})	25 (TP µg L^{-1})	% Change	% Change by Hossain et al. (2019)
Phytoplankton (mm^3 L^{-1})	4.56	3.44	−24.6 %	
Zooplankton (mg m^{-3})	169	148	−12.2 %	
Planktivores (g m^{-2} gillnet)	6.73	3.70	−45.0 %	−67.0 %
Benthivores (g m^{-2} gillnet)	36.3	37.0	2.0 %	
Piscivores (g m^{-2} gillnet)	25.6	25.2	−1.2 %	−22.2 %

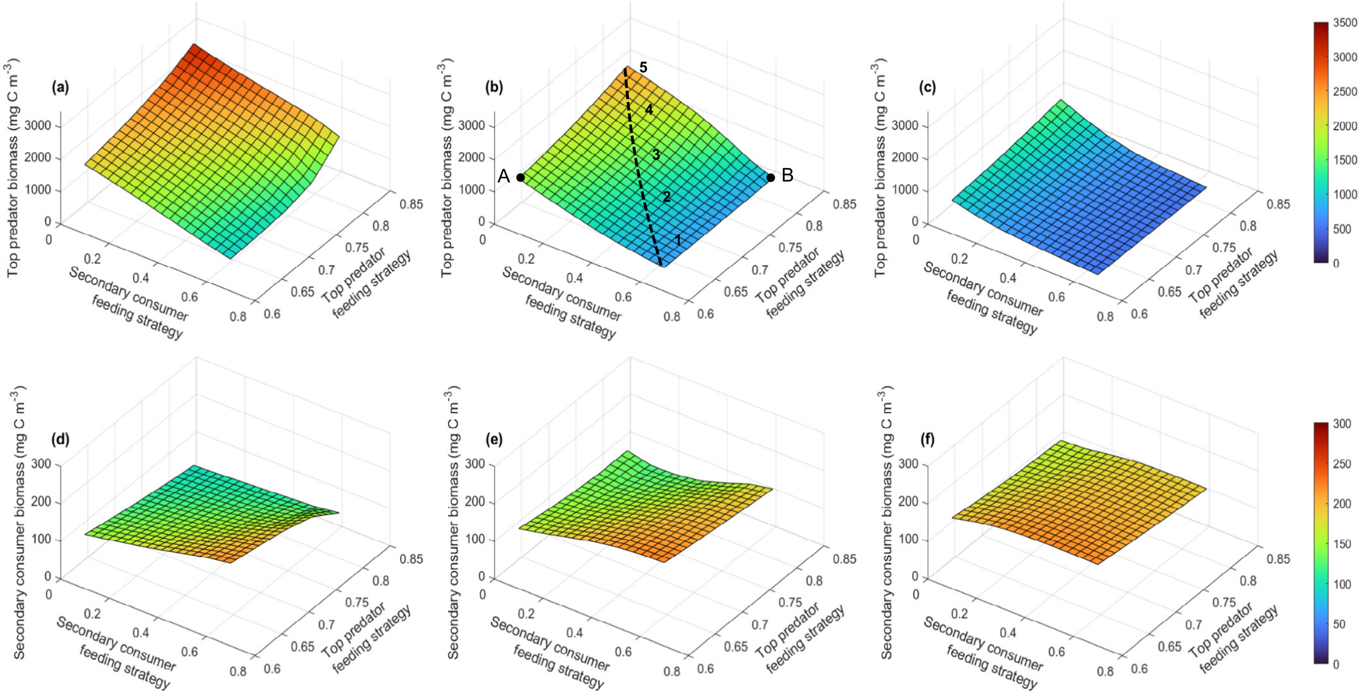

Fig. 4. Response surface for fish biomass as predicted by the process-based food-web model. X-axes correspond to the fractional preference of the secondary consumer to feed on zooplankton, representing the transition from benthos- ($pref_{(zooppl)} \rightarrow 0$) to zooplankton-dominated diet ($pref_{(zooppl)} \rightarrow 0.8$). Y-axes correspond to the fractional preference of the top predator to feed on the secondary consumer, indicating an increasing reliance upon the secondary consumer ($pref_{(planpi)} \rightarrow 0.85$) relative to a zooplankton- and/or benthos-dominated diet ($pref_{(planpi)} \rightarrow 0.6$). Z-axes show the predicted top predator (*a-c*) and secondary consumer (*d-f*) biomass. Fish biomass was predicted based on three nutrient loading scenarios: +50% (*a* and *d*), present (*c* and *f*), and −50% (*b* and *e*) of the prevailing loading conditions in the Bay of Quinte. Black dotted line corresponds to a gradient of feeding strategies spanning from (1) shared/overlapped to (5) diverse or distinctly different diets between secondary consumer and top predator. Point A represents a scenario of non-pelagic food consumption of the secondary consumer and zooplanktivory for the top-predator, while point B represents piscivory for the top predator and zooplanktivory for the secondary consumer.

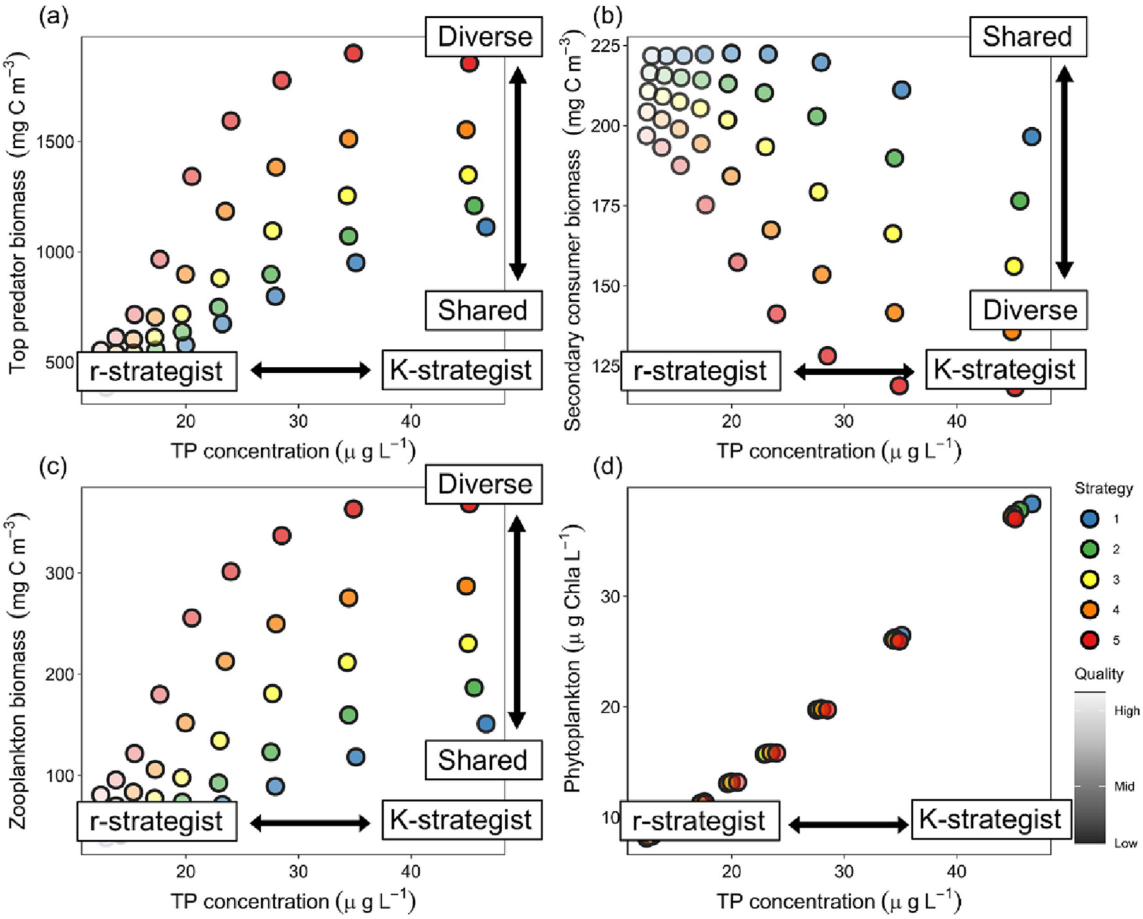

Fig. 5. Total phosphorus-biomass relationships simulated under a range of feeding strategies and food-quality scenarios. Circles represent the predicted average biomass of the (*a*) top predator, (*b*) secondary consumer, (*c*) zooplankton, and (*d*) phytoplankton (using chlorophyll *a* as a proxy). The color gradient represents the feeding behaviour of the two simulated fish groups; namely, "shared" (1, blue) to "diverse" (5, red) diets between secondary consumer and top predator. Strategy numbers 1 to 5 correspond to the scenarios presented in panel (4b), where the two trophic guilds of the fish assemblage display strong resource competition (strategy 1; zooplanktivory by both top predator and secondary consumer) and gradually shift to a minimal diet overlap (strategy 5; piscivorous top predator and non-planktivorous secondary consumer). Food quality ranges from the high food quality of a diatom-like (r-strategist) group to the poor food quality of a cyanobacteria-like (K-strategist) group. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

assemblage dominated by r-strategists results in distinctly steeper slopes for the top predator biomass-TP relationship compared with the slopes realized when the algal assemblage resembles K-strategists (Fig. 6a). Importantly, our analysis also highlighted the presence of a "sweet spot" between the two distinct characterizations of r- and K-strategists, where optimal food quantity and quality conditions are achieved, thereby sustaining the highest levels of fish biomass (Fig. 6b).

Discussion

Prompted by cultural eutrophication and the need to improve the quality and aesthetics of our freshwater resources, the mandated programs to curtail P inputs were successful in triggering the process of oligotrophication. This process generally brought about a decline in primary productivity, dominance of smaller-sized phytoplankton, discernible increase in water clarity, and increased macroinvertebrate activity (i.e., Ludsin et al., 2001). In the Great Lakes, however, the net impact of oligotrophication is convoluted by a multitude of stressors, including the establishment of the invasive filter-feeding dreissenid mussels and benthic-feeding round goby (Mills et al., 2003). In particular, the combined effects of oligotrophication and dreissenid-induced modifications have been conducive to the prevalence of benthic over pelagic energy pathways, which in turn favor the prevalence of bottom-dwelling organisms and fish communities that make efficient use of the benthic habitat (Johnson et al., 2005; Hogan et al., 2007). This documented shift in importance of benthic processes, the so-called benthification, is likely more pronounced in the more diverse and highly productive nearshore and embayment habitats (Sabel et al., 2020), such as the Bay of Quinte in Lake Ontario. Viewed from this perspective, our study used a combination of statistical and process-based modelling to corroborate the gradual shift in the trophodynamics in this shallow embayment and examine the potential impact of two major oligotrophication mechanisms on the integrity of fisheries; namely, the capacity of structural shifts in the algal assemblage to regulate the flow of energy through the food web, and the increasing importance of benthification processes coupled with the potential role of fish feeding strategies to make-up for the gradual decline of pelagic biogenic production.

Benthification processes and diversification of trophodynamics in the littoral zone*:* Our SEM analysis is suggestive of a modest role of the conventional food-chain pathway between primary (zooplankton) and secondary (planktivorous and benthivorous fish) consumers, as well as between pelagic secondary consumers (i.e., planktivorous fish) and top predators in the Bay of Quinte during the two time stanzas examined (Fig. 3, Table 1). In contrast,

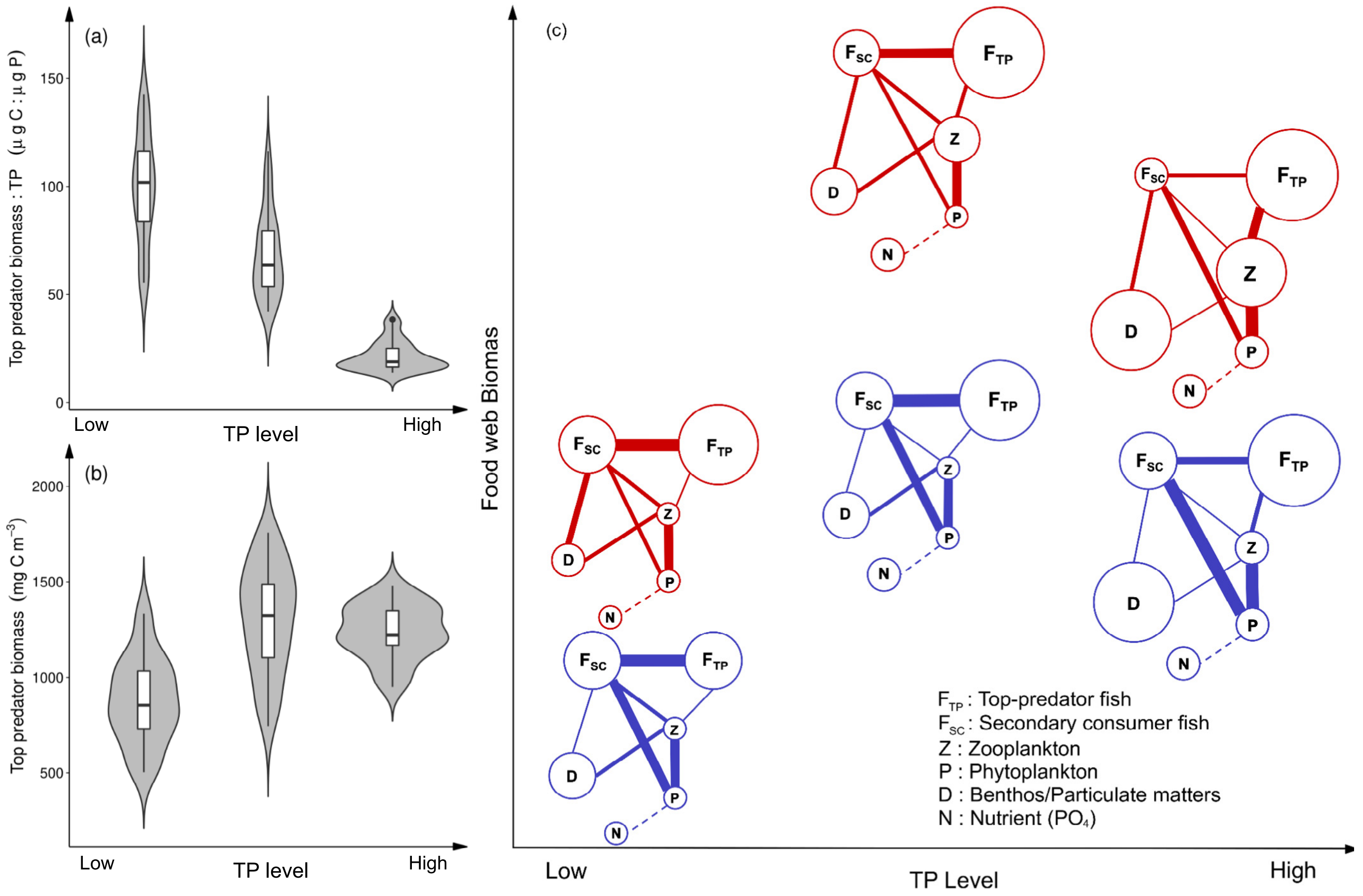

Fig. 6. Top predator trophic efficiency, biomass, and food-web structure described as P fluxes across a range of ambient nutrient availability. The hybrid violin-box plots show (*a*) the slopes of the top predator versus TP relationships and (*b*) top predator biomass simulated under a range of feeding strategies and phytoplankton specifications (r, default, and K strategists). The outline of shaded areas are the kernel density estimation of the calculated slope and biomass. Panel (*c*) illustrates the food web structure derived from the P fluxes among the simulated biotic compartments under two fish feeding strategies; "shared" (red) and "diverse" (blue) diets for the secondary consumer and top predator. The size of the circles represents the relative biomass size of each biotic compartment across the fish feeding strategies and algal assemblage characterization. The thickness of the lines denotes the strength of the corresponding trophic relationship. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

despite the phytoplankton biomass decline achieved from nutrient control, herbivorous consumption fuels the planktivorous fish assemblage, which in turn appears to be disconnected from piscivorous fish and this bottleneck may have been exacerbated by the invasion of dreissenids. The general consensus in the limnological literature is that the establishment of dreissenid mussels acted as a catalyst of oligotrophication and benthification. Owing to their capacity to filter large volume of water (Fanslow et al., 1995), their high filtration rates of seston and growth (Haag and Garton, 1992) and potential to ingest a wide range of particle sizes of suspended biogenic material (Vanderploeg et al., 2001), dreissenid mussels contribute to the sequestration of the external resource subsidies in the littoral and profundal zones, which in turn accelerates the benthification of the nearshore zone and oligotrophication of the pelagic environment (Cha et al., 2011). Nevertheless, the rapid proliferation of round goby and their voracious consumption of mussels and other benthic prey items has led to the establishment of an alternative pathway of energy that could, in principle, support the upper food web (Truemper and Lauer, 2005; Johnson et al., 2005; Campbell et al., 2009), consistent with empirical evidence from the Bay of Quinte (Hoyle et al., 2017).

Interestingly, our hierarchical SEM provided evidence of a consistently strong coupling between benthivorous and piscivorous fish before (Fig. 3a) and after (Fig. 3b) the invasion of the two bottom dwellers (dreissenids, round goby) in the Bay of Quinte (Table 1). In fact, the path coefficient that links the two trophic guilds was somewhat higher during the pre- (β_7 = 0.884) relative to post-dreissenid (β_7 = 0.624) invasion period. Given that the majority of the data (i.e., 15 out of 17 years) used to derive the pre-invasion posterior coefficient span the period after the P abatement in the bay, the distinctively strong linkage between the two trophic guilds may suggest that the benthification processes were initiated earlier and independently from the establishment of invasive mussels. The top predators of the fish assemblage potentially adapted to the gradual decline in pelagic biogenic production by diversifying their feeding ground from pelagic to benthic habitats. A characteristic example is walleye, the dominant piscivorous -and very popular for the local recreational anglers- fish in the Bay of Quinte (ESM Fig. S8), known to display generalist foraging behavior with documented dietary flexibility in littoral environments; especially when turbid/low light availability conditions prevail (Jones et al., 1994; Hoyle et al., 2012; Herbst et al., 2016). Only six years after the introduction of rainbow smelt in Horsetooth Reservoir, Colorado, walleye diet was recorded to have shifted from 55% salmonids and 23–26% invertebrates to entirely consisting of rainbow smelt, which in turn resulted in an increased growth of juveniles (age 1 to age 3) by 50 % (Jones et al., 1994). Stomach content and stable isotope analysis of walleye from both pelagic and littoral habitats in four inland oligotrophic lakes that drain into Lake Huron signified their tendency to feed upon the most abundant food sources and rely more frequently on littoral prey items (Herbst et al., 2016). In particular, the Bay of Quinte walleye diet has been found to be distinctly more diverse than that for Lake Ontario, comprising alewife, yellow perch, white perch, gizzard shad, and johnny darter (*Etheostoma nigrum*), while round goby can account for an average frequency of occurrence between 15 and 20% (Hoyle et al., 2017).

Alewife has been the predominant food staple for walleye, representing one-half of their diet in the Bay of Quinte and nearly the entire diet in eastern Lake Ontario (Hoyle et al., 2017). Alewife abundance declined in 1977–1978 in the Bay of Quinte, largely due to a severe winter in 1977, followed by a strong year-class of yellow perch that typically displays a partial diet overlap with alewife (Minns and Hurley, 1986). While the long-term abundance of alewife in the lower bay displayed fluctuations with discernible recovery periods (i.e., early 1980s and recent years), the population in the upper and middle bay continued to decline and has never been fully restored (Currie et al., 2020). Nevertheless, the abundance of piscivorous fish in both upper and middle segments of the Bay of Quinte appeared to have stabilized after the mid-1990s, even with the extremely low alewife prey availability (Currie et al., 2020). One of the plausible explanations for the relatively stable piscivorous fish community is the presence of benthivorous white and yellow perch after the replacement of the zooplanktivore alewife and herbivorous gizzard shad in the early 1980s (see ESM Fig. S8). Both white and yellow perch are known to be facultative zooplanktivores, feeding on zooplankton during certain period of their life cycles, but mainly relying on benthic food items at young life stages (Danehy et al., 1991). By contrast, the diet of young-of-the-year (YOY) alewife is dominated by zooplankton, comprising mainly cyclopoid and occasionally calanoid copepods (Strus and Hurley, 1992; Urban and Brandt, 1993). In the virtual environment of our process-based model, combinations of feeding strategies assigned to two coexisting fish trophic guilds profoundly affected fish productivity. Within the range of parameters assigned, when the secondary consumer feeds upon benthos/-particulate matter sources (>70%) and zooplankton accounts for less than 30% of their diet, the biomass of the top-predator can be effectively sustained, even if their diet heavily relies on the secondary consumer (70–75%) (Fig. 4c). Thus, the findings from our process-based model are on par with the trends observed in the upper and middle segments of the Bay of Quinte, signifying that the predominance of benthivores can compensate for undesirable trends in planktivorous fish. In fact, our analysis suggests that piscivory is a reliable foraging strategy for the top predator, as long as the secondary consumer does not opt for a zooplankton-dominated diet. Interestingly, in the latter scenario, our analysis showed that the trophic state of the system (or food availability) emerges as an important covariate that determines the standing biomass of the top predator (see variations between Fig. 4a-c and following discussion).

Phytoplankton structural shifts and food-web productivity: Understanding the potential mechanisms that influence aquatic ecosystem productivity and stability is critical for both water resource and fisheries management (Schulz et al., 2004). One of the major adverse attributes of phytoplankton assemblages dominated by cyanobacteria is the decoupling of trophic interactions (Gulati and Demott, 1997). Cyanobacteria are known to constrain zooplankton grazing due their morphological characteristics and production of toxic metabolites that reduce ingestion rates (Gliwicz and Lampert, 1990; Rohrlack et al., 1999), as well as their poor nutritional value that negatively affect the growth and reproduction of primary consumers (Müller-Navarra et al., 2000; von Elert et al., 2003). Unlike eukaryotic algae, cyanobacterial cells have low lipid content (von Elert et al., 2003) and minimal amounts of polyunsaturated and other essential fatty acids (Müller-Navarra et al., 2000) that are only synthesized by autotrophs, but are critical for the metabolism and functioning of food-web consumers. Following the gradual prevalence of oligo/mesotrophic conditions in the Bay of Quinte, our modelling experiments examined the hypothesis that a shift towards a diatom-dominated phytoplankton assemblage with higher nutritional quality (r-strategist) may compensate for reduced food availability and more effectively support overall ecosystem productivity. The model signified the role of food abundance as a primary factor shaping fish production, but the realized fish biomass levels can be modulated by the interplay between the nature of the algal assemblage and the degree of diet overlap among the co-existing fish trophic guilds (Fig. 6c). Recreating a eutrophic environment associated with the prevalence of a cyanobacteria-dominated (K-strategist) autotrophic community led to food-web destabilization, whereby the standing biomass of the top predator could vary significantly depending on the degree of diet overlap with the secondary consumer. In contrast, the importance of fish feeding strategies was decisively dampened when a fast-growing, high nutritional quality phytoplankton prevailed. Interestingly, while the latter scenario was associated with the highest top-predator biomass per unit P ratios, our analysis pinpointed the presence of a "sweet spot" along the phytoplankton continuum, lying between the two distinct characterizations of r- and K-strategists, where we achieved the optimal balance of food quantity and quality and consequently the highest levels of fish biomass (Fig. 6c).

In response to P control, total phytoplankton biomass significantly declined throughout the Bay of Quinte, but the most dramatic compositional changes occurred after the invasion of dreissenids (Shimoda et al., 2016). Specifically, the spring bloom, originally dominated by genera from the classes of *Bacillariophyceae* (*Synedra* spp., *Stephanodiscus* spp., *Aulacoseira* spp.) and *Chrysophyceae* (*Dynobryon* spp.), has practically disappeared. The relative contribution of *Stephanodiscus* spp. and *Fragilaria* spp. to the total algal biovolume, two of most dominant diatom genera, also decreased over the course of our study period. The same pattern held for species of the genera *Cryptomonas* and *Rhodomonas*, which are perceived to have high nutritional value and their decline may have profound implications for the broader food-web functioning (Shimoda et al., 2016). By contrast, owing to their growth pattern (long multi-cellular trichomes), the relative impact of dreissenid filtration may not have been as pronounced for the two major *Aulacoseira* species (A. *granulata* and A. *ambigua*), and consequently they still account for a fairly high proportion of total phytoplankton. Additional effects include the replacement of N_2-fixing genera, such as *Anabaena* spp. and *Aphanizomenon* spp., by the non-N_2 fixer *Microcystis* spp. in the summer phytoplankton assemblage (Kelly et al., 2019). Thus, while we may not be able to characterize unequivocally the overall phytoplankton palatability for zooplankton in the Bay of Quinte, it stands to reason that many of these compositional shifts were not conducive to establishing a tighter trophic coupling between primary producers and herbivorous zooplankton, despite the success in controlling P loading from the surrounding watershed.

Consistent with the previous assertion, our analysis downplayed the significance of zooplankton as an important link between primary producers and larger heterotrophs such as predatory invertebrates and planktivorous fish, and consequently as a pathway of energy to the upper food web. The Bay of Quinte is a productive environment for zooplankton compared to other littoral environments in the Great Lakes, with cladocerans (*Bosmina*, *Eubosmina*, *Daphnia retrocurva*, *D. galeata mendotae* and *Chydorus sphaericus*) being the typical dominant group of the summer assemblages (Bowen and Johannsson, 2011; Johannsson and Bowen, 2012). Using a series of indicators (e.g., cladoceran mean size, *Chydorus* biomass, Shannon Diversity Index, abundance of rotifers, percent large *Daphnia*) that capture both top-down (intense planktivory) and bottom-up (dominance of eutrophic species) impacts, Currie et al. (2020) noted that the zooplankton community displayed an improvement between the pre- and post-P control periods during late 1970s/early 1980s, when nutrients and planktivory were very high, but appears to have stalled ever since. Overall, the same study asserted that there was neither strong evidence of strong grazing effects on zooplankton by planktivorous fish (alewife, gizzard shad, spottail shiner) nor a strong coupling between algae and zooplankton, which was partly attributed to the persistence of inedible colonial cyanobacteria (e.g., species of *Microcystis*, *Gloeotrichia*) that interfere with the transfer of energy to the upper trophic levels (Currie et al., 2020). To reconcile this bottleneck within the planktonic food web in the Bay of Quinte, the role of the microbial loop (bacteria, autotrophic picoplankton, heterotrophic nanoflagellates and ciliates) has been invoked as a potential pathway to modulate the transfer of energy from lower to higher trophic levels (Munawar et al., 2011). In the Bay of Quinte, heterotrophic nanoflagellates frequently contribute more biomass to the planktonic food web than phytoplankton and zooplankton combined, and their utilization of food resources (bacteria and autotrophic picoplankton) that would otherwise have been available to zooplankton may be another explanation why *Daphnia* biomass is still supressed (Munawar et al., 2011). Thus, while there is still considerable debate as to whether heterotrophic micro-organisms provide a link for the transfer of organic carbon to higher trophic levels or serve as a sink for remineralization of organic carbon (Brett et al., 2017), the strong SEM path from phytoplankton to planktivorous fish still signifies the positive impact of the planktonic food web on their biomass. The weaker relationship between zooplankton and planktivores may suggest that the degree to which fish capitalize upon the increased productivity of the system could be associated with more complex pathways or simply that the zooplankton variable used (total carbon biomass) to recreate its role within the broader food web is not the best proxy, e.g., a length-weighted zooplankton density could have offered a more accurate surrogate variable for that matter (Arhonditsis et al., 2004).

Structural complexity of the littoral environment-Fish migration patterns: The structural complexity of the littoral environment is another confounding factor that modulates the response of individual fish species to oligotrophication. Notably, the benthic macroinvertebrate abundance in shallow systems tends to be distinctly higher than in deep lakes (Jeppesen et al., 1997). Even more so, the benthic productivity could increase in shallow habitats due to improved oxygenation and light availability, following the nutrient regulation and phytoplankton biomass reduction. The recovery of macroinvertebrates (e.g., *Hexagenia* spp.) on the soft sediments of the shallow western basin of Lake Erie is a case in point (Ludsin et al., 2001). Likewise, water quality improvement in the Bay of Quinte triggered an increase in the diversity of the benthic community with the reappearance of epibenthic species (*Pisidium*, *Amphipoda*, *Gastropoda*), as well as a gradual compositional shift toward smaller species of oligochaetes and chironomids typically requiring higher oxygen concentrations than larger species that use haemoglobin to store oxygen for later use (Dermott et al., 2012). Interestingly, counter to the modest macrophyte response to point-source P control, the significant increase of light penetration, stemming from dreissenid filtration, appears to have been the primary catalyst for the excessive growth of submerged macrophytes and the rapid expansion of existing shallow-water beds into the deeper waters of the Bay of Quinte (Leisti et al., 2012; Kim et al., 2013). The submerged aquatic vegetation represents favourable fish spawning and nursery habitat, refuge from predation, as well as a feeding site because macrophytes provide habitat for macroinvertebrates (Eklöv, 1997). The improved illumination of the water column and expansion of aquatic vegetation has been associated with the decline in walleye abundance (with documented preference for low light environments) and a discernible increase in the abundance of sunfish species, e.g., pumpkinseed (*Lepomis gibbosus*), bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and largemouth bass (*Micropterus salmoides*) (Hossain et al., 2019).

The establishment of invasive species has not consistently led to positive improvements in the state of the benthic community in the Bay of Quinte. Competition with dreissenids may have been responsible for the reduction of the filter feeding polychaetes and *Sphaerium* clams, which originally benefitted by the changes in the littoral environment brought about by P control. More importantly, the extirpation of cold- (*Diporeia*; lower bay) and warm-water (*Gammarus*; upper bay) amphipods, both favourable staples of the diet of bottom-feeding fish, has been attributed to the collective pressure from food competition with dreissenids and voracious predation by round goby (Dermott et al., 2012). The documented inability of *Diporeia* to receive organic matter from the water column and increase in abundance is likely one of the factors that may have accelerated the declining trend of planktivores in the system, which depend on *Diporeia* as an important food source (Burlakova et al., 2023). Thus, although historical information on benthic fauna or fish diet data does not allow us to consolidate the evolution of the trophodynamics in the Bay of Quinte over time, the gradual predominance of benthivorous over planktivorous fish during the post-P control period (Hoyle et al., 2012; Hossain et al., 2019) may be attributed to changes in the benthic assemblage that could have (directly and/or indirectly) made up for the gradual decline of biogenic productivity. Owing to the lack of a continuous time series for benthic biomass, we opted for a typically used proxy of the trophic status of the system (ambient TP levels), which was also found to display a positive relationship with the benthic productivity in the middle and outer Bay of Quinte (see Fig. 3 in Dermott et al., 2012). Our SEM analysis signified an important energy pathway (TP → benthivores) fueling the trophodynamics that differ from classic pelagic food chain, whereby primary producers support primary consumers (Fig. 3), which in turn fuel secondary consumers and ultimately the top predators. As previously mentioned, the same pattern was reinforced by our theoretical modelling, as greater reliance on alternative food sources, such as benthos, autochthonous or even allochthonous particulate matter, not only provided a viable scenario for the sustenance of the secondary consumer but also led to thriving top predators, when their diet was sufficiently diversified (Fig. 4).

One factor that our analysis did not account for in detail is the role of terrestrial organic matter inputs in supporting the production of invertebrate and fish consumers in lakes. Counter to the popular notion suggesting allochthony is an important subsidy for animal consumers (Cole et al., 2006; Prairie, 2008), Brett et al. (2012) carried out a meta-analysis of studies that reported terrestrial carbon mass influx and algal primary production data for lakes with total phosphorus $\leq 20\ \mu g\ L^{-1}$ (i.e., distinctly lower than the levels in the Bay of Quinte), and indicated that autochthonous production is 4–7 times greater than the flux of terrestrial basal resources available to consumers in oligo- or mesotrophic lakes. Thus, if we factor in the recalcitrant biochemical composition of terrestrial carbon along with the eutrophic or upper-mesotrophic state of the Bay of Quinte during the study period, we believe that the support of upper trophic level production by allochthonous organic matter inputs must have been negligible or could have played some role only when essential biomolecules typically synthesised by algae were available (Brett et al., 2017). Another critical factor that was not explicitly accounted for by either of the two modelling strategies used is the well-documented annual fish migration patterns (especially for mature walleye) which are thought to be related to avoidance of warm temperatures in the upper segment of Bay of Quinte (Bowlby and Hoyle, 2011; Elliott et al., 2022). In this regard, Hoyle et al. (2017) showed a distinct diet shift that leads to an increase in the relative weight of walleye foraging on abundant alewife prey in the lower bay and eastern Lake Ontario during summer, which underscores the importance of alewife availability in maintaining a large and productive Bay of Quinte walleye population. Nonetheless, unlike walleye, other piscivores in the system, including northern pike, bowfin, longnose gar, largemouth and smallmouth bass do not consistently migrate to Lake Ontario, mainly relying on food sources in the Bay of Quinte, and as such could be directly amenable to the feeding adaptation strategies and alterations of the trophodynamics examined in the present study.

On a final note, we caution that considerable uncertainty surrounds the practice of basing fish biomass forecasts on simple regression models with TP concentrations as the key predictor. Especially in littoral environments, these types of relationships may not necessarily be of causal nature, but rather represent simple correlations that collectively reflect a variety of complex and multi-faceted anthropogenic influences, fish-life histories and their ecological interactions on the variability of fish assemblages. Moreover, the generation times (or turnover rates) of organisms at the lower food web could be closely related to the prevailing abiotic conditions, but longer-lived and mobile top predators may be less responsive to short-term variations and have the ability to adapt to long-term trends. For example, the period (1977–1978) with the sharpest decline of the ambient TP levels in the Bay of Quinte coincided with a major winter-kill event of white perch, which led to a strong year-class of walleye and subsequently to a fish community characterized by abundant walleye with high growth rates (Hoyle et al., 2012). This shift to dominance by piscivores effectively controlled the formerly hyper-abundant prey species (e.g., alewife) during the 1980s, but the density-dependent effects, i.e., the growth rate of young walleye was dependent upon their numbers in the population, affected the distribution and availability of resources and may have led to a decline in walleye by the early 1990s. The latter trend was further exacerbated by the establishment of dreissenid mussels, whereby the increased water transparency and macrophyte proliferation created conditions conducive to the prevalence of warm-water species, such as alewife, largemouth bass, sunfish, white and yellow perch, in favour of the light-sensitive walleye (Chu et al., 2004; Lester et al., 2004). Moreover, a new line of evidence from trawling programs suggests that the main cause for the decline in walleye, since the establishment of dreissenids, has been the decreased survival of young walleye (less than 3 months old), which are independent of the changes in adult growth and abundance (Lantry et al., 2014). Coupling these wax-and-wane cycles of the walleye population over the course of our study period with the nearly monotonic decline of TP concentrations during the 1980s and 1990s, followed by a pattern of significant year-to-year variability around the level of 30 $\mu g\ L^{-1}$ thereafter, initially resulted in a distinctly negative, followed by a strong and then a weaker positive relationship between the two variables, although their trends were largely shaped by different drivers (Hossain et al., 2019; Arhonditsis et al., 2019).

Conclusions-Implications for fisheries management: A multitude of ecological mechanisms can modulate the potential adverse impacts of oligotrophication on the integrity of fish assemblages in littoral environments. Desirable plankton composition shifts and dietary diversification can prolong the sustainability of fisheries after the establishment of nutrient-deficient conditions and low biogenic production, without the need to invoke the role of processes that draw upon basic principles of fish ethology (e.g., migration patterns) or ontogeny (e.g., age, size structure, biochemical adaptation). The present study provided evidence that the benthification processes in the Bay of Quinte may have initiated shortly after P control in the late 1970s and independently from the invasion of exotic species. The invasion of dreissenids and round goby during the 1990s led to the establishment of a new trophic pathway that could act as an additional buffer to the variability of the trophodynamics among primary producers, primary and secondary consumers by fueling the upper food web with benthic energy. Our analysis further suggested that the degree of diet overlap between competing trophic guilds of fish can significantly modulate their productivity. Specifically, when the secondary consumers depend on benthic food items and the top-predator is predominantly piscivorous, fish production is consistently high, even when oligotrophic conditions prevail. The prevalence of fish species (e.g., white perch, yellow perch) that mainly rely on benthic food items at young life stages, following the decline of the zooplanktivore alewife and herbivorous gizzard shad in the early 1980s, along with the distinct evidence of a more diverse walleye diet in the Bay of Quinte relative the offshore waters of Lake Ontario lend support to our initial hypothesis. The latter finding could also provide a plausible explanation for the modest contribution of the zooplankton community to the broader trophodynamics and their apparent disconnect from the profound disturbances that took place over the time span studied.

The composition of the autotrophic community induced by oligotrophication is another major confounding factor that can shape food web productivity patterns. The gradual prevalence of an algal assemblage dominated by r-strategists of high nutritional quality (or a diatom-based food web) results in distinctly steeper slopes for the top predator biomass-TP relationship and higher food web stability, compared with the lower biomass production per P unit available and inherent uncertainty registered when the phytoplankton community resembles to a (cyanobacteria-like) K-strategist. Importantly, the phytoplankton community structure can achieve an optimal balance between abundance and composition, where food quantity and quality maximize the benefits for fish productivity and reach the highest biomass levels. Moreover, notwithstanding the considerable amount of terrestrially derived carbon available in the littoral environment of the Bay of Quinte, the recalcitrant biochemical composition of this material should be a major impediment for its broader use for fish production relative to algal basal resources.

Counter to Hossain et al.'s (2019) predictions, our analysis predicted a moderate decline in fish biomass, if the proposed reduction of the seasonal ambient TP levels from 30 to 25 $\mu g\ L^{-1}$ is realized. Empirical (data-driven) equations that directly use TP concentrations as a predictor for fish biomass are intended to collectively capture the impact of a suite of mechanisms that could conceivably operate in the littoral zone and may thus be prone to greater uncertainty than in pelagic environments. Even when their explanatory power appears to be high, the depicted relationships can be of correlative (instead of causal) nature, and as such they may not be suitable for forecasting future fish population responses. On-going remedial action plans to mitigate non-point source pollution are expected to improve water quality and may not necessarily trigger a collapse of the fish community in the Bay of Quinte. Combination of empirical evidence and modelling suggests that many local fish species of commercial and recreational importance (walleye, largemouth bass, northern pike) can modify their dietary and behavior patterns and maintain their population levels.

CRediT authorship contribution statement

Yuko Shimoda: Conceptualization, Formal analysis, Visualization, Writing – original draft. **Haibin Cai:** Formal analysis, Writing – original draft. **Yasasi Fernando:** Formal analysis, Writing –

review & editing. **Akunne Okoli:** Formal analysis, Writing – review & editing. **Zhuowei Xu:** Formal analysis, Visualization. **Marten Koops:** Conceptualization, Writing – review & editing. **Timothy B. Johnson:** Conceptualization, Writing – review & editing. **George B. Arhonditsis:** Conceptualization, Formal analysis, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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