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Depensation in fish recruitment driven by context-dependent interactions with another predator

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ABSTRACT

Recruitment depensation describes elevated juvenile mortality with declining adult population size which can prevent or delay stock recovery. Understanding the factors influencing when a population undergoes depensation provides resource agencies with targets for management action. Using estimates of depensation from 28 walleye (*Sander vitreus*, Percidae) populations in Wisconsin identified by Sass et al., (2021), we tested for potential abiotic and biotic predictors of walleye recruitment depensation. The best fitting model contained covariates for climate, land cover, and fish community composition, all interacting with the relative abundance of largemouth bass (*Micropterus salmoides*, Centrarchidae). The consistent interaction effect of largemouth bass across the other covariates suggests a key role of this species in regulating walleye recruitment dynamics at low population size. The risk of depensation was negatively correlated with largemouth bass abundance in our dataset, pointing towards continued challenges for walleye populations given the increasingly favorable social and environmental conditions for largemouth bass. Using the model, vulnerability to depensation was predicted for an additional 115 walleye lakes with insufficient data to directly estimate the risk of depensation. Predictions suggested that 73 prediction lakes are vulnerable to depensatory recruitment should population sizes significantly decrease. This predictive framework could be used to prioritize lakes for different management actions based on depensation strength and average adult population size. Lakes with low walleye abundances, but low risk of depensation, may be more likely to respond positively to management efforts and are likely better candidates than those where depensation effects are likely strong when abundance is low.

1. Introduction

A prevailing paradigm in managing fish and wildlife populations, including commercial and recreational fisheries, assumes that juvenile survivorship increases as adult population size declines (i.e., compensatory recruitment; Hilborn and Walters, 1992; Ricker, 1975; Neave, 1953; Allee, 1941; Herrando-Pérez et al., 2012). However, no relationship between adult abundance and juvenile survival has also been documented in several species (Allen et al., 2011; Dawson and Jones, 2009; Hilborn and Walters, 1992). More importantly, elevated juvenile mortality with declining adult population size (i.e., Allee effects), can also occur under certain abiotic and biotic conditions when adult

abundance falls below a critical threshold (Allee, 1941; Kramer et al., 2009; Neave, 1953; Ricker, 1975, 1963; Sass et al., 2021). Allee effects, or as they are also known - recruitment depensation - threatens fish and wildlife populations because as population sizes are reduced through harvest or other interacting factors, a population may become trapped in a positive feedback loop where declining recruitment, as a result of declining adult abundance, leads to further recruitment declines (Hilborn and Walters, 1992). This phenomenon can not only slow or prevent populations from recovering from low abundances, but also lead to extirpation in the absence of intervention (Cahill et al., 2022; Kramer et al., 2009; Post et al., 2002; Walters and Kitchell, 2001). Understanding whether and when depensation occurs can allow natural

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resource agencies to institute interventions and regulations to prevent abundances from declining to levels where depensation is a risk, or to restructure communities to increase resilience against drivers of depensation (Cahill et al., 2022).

Empirical observations of recruitment depensation are rare (but see Keith and Hutchings, 2012; Sass et al., 2021) and the drivers behind depensation explored even less. Yet, the phenomenon has long been theorized and often implicated in the collapse of fisheries and their failure to recover following reductions in or cessation of harvest (Liermann and Hilborn, 2001, 1997; Myers et al., 1995; Post et al., 2002; Ricker, 1963, 1954; Walters and Kitchell, 2001). Recruitment depensation is thought to arise as a result of one of three mechanisms: 1) reduced probability of fertilization (i.e., difficulty finding a mate at low adult population size); 2) impaired group dynamics (i.e., reduced survival or foraging efficiency as school size declines); and 3) conditioning of the environment (i.e., reduced abundances are unable to structure the environment to their benefit through foraging effects, also referred to as ‘cultivation’ or ‘predator pits’) (Liermann and Hilborn, 2001; Walters and Kitchell, 2001). The key difficulty in identifying depensation in fisheries is the lack of fisheries-independent data available to characterize trends in juvenile survival at low adult population sizes where a depensatory threshold might be identified (Keith and Hutchings, 2012). The precise adult abundance at which this critical depensation threshold occurs likely varies among populations, but in general, will likely be very low. In marine stocks, Keith and Hutchings (2012) suggested 20% of the maximum observed population biomass as a conservative threshold for depensation risk based on a review of 207 marine fish populations. Further, depensatory thresholds may differ among individual populations of the same species due to the abiotic and biotic characteristics of the waterbodies they inhabit (Rypel et al., 2019, 2018; Sass et al., 2021; Tsehaye et al., 2016).

Throughout the upper Midwestern USA and Canada, walleye (*Sander vitreus*, Percidae) are a highly valued recreational sportfish and tribal subsistence species that is primarily targeted for harvest (Boehm et al., 2022; Gaeta et al., 2013; Mrnak et al., 2018). Given recent declines in natural recruitment, walleye fisheries are at risk of overharvest (Embké et al., 2019; Rypel et al., 2018). Additionally, recent research has shown that many walleye populations are at risk of depensatory recruitment should adult abundances decline, such as those associated with exploitation and other environmental influences (Sass et al., 2021). The immense cultural, recreational, and economic value of walleye in the region underscores the importance of understanding mechanisms influencing recruitment. How these challenges are met will have wide-ranging influences in the region, particularly in places where they support a tribal subsistence harvest season and a recreational angling fishery (Shultz et al., 2022; U.S. Department of the Interior, 1991). To better understand drivers of recruitment depensation in walleye, which have not been previously examined, we use the Wisconsin walleye fishery as a data-rich system to explore this important dynamic.

Recruitment depensation in walleye populations might plausibly be influenced by several factors. Liermann and Hilborn (2001) described two factors that relate specifically to recruitment at low adult population sizes. These factors are a reduced ability to condition the environment in favorable ways relative to a competing species, in this case through predation effects on other species, and impaired group dynamics that limit foraging or increase predation risk. Separately, some factors which may drive recruitment depensation influence recruitment regardless of population size. For example, variation in watershed land cover and within-lake habitat could influence walleye recruitment via multiple avenues (i.e., thermal-optical habitat and structural predation refuge; Lester et al., 2004; Sass et al., 2017; Raabe et al., 2020). Warming temperatures due to climate change are predicted to negatively affect recruitment of walleye populations regardless of adult abundance (Hansen et al., 2015a, 2018). Generally, walleye recruitment (i.e. survival from spring hatch to the first fall of life) has often been best explained by environmental factors (Beard et al., 2003; Zachary S Feiner

et al., 2022; Hansen et al., 1998; Shaw et al., 2018). However, it is important to note that we differentiate between factors influencing recruitment in general, regardless of population size, and factors affecting recruitment at low population sizes where depensation can occur. Here, we aim to better understand potential abiotic (climate and land use) and biotic (adult abundance, community composition, and competitor abundance) factors influencing walleye recruitment depensation rather than recruitment as a whole (which has been extensively explored, see Hansen et al., 1998, 2018; Beard et al., 2003; Tsehaye et al., 2016; Shaw et al., 2018; Feiner et al., 2019; Raabe et al., 2020). This distinction is noted elsewhere (Hutchings, 2014; Keith and Hutchings, 2012) and is key to better understanding the dynamics of depleted populations and potential strategies for conservation and rehabilitation. Strategies for conservation and rehabilitation will focus on whichever factors might be feasibly influenced by a fishery manager (Carpenter et al., 2017). Some of the factors explored here (i.e., conditioning the environment and impaired group dynamics) could be influenced by a fishery manager through manipulations of the fish community to reduce competition and predation on walleye. Conversely, land cover and climate change are not typically under the direct influence of a fishery manager (see Jacobson et al., 2013 for a notable exception) but over the long term may be able to be influenced. In this way, understanding the mechanism(s) driving recruitment depensation in walleye are important for managing this species and any species undergoing population declines to a level where depensation may slow or prevent recovery.

Using recently published estimates of depensation for 28 walleye populations in the Ceded Territories of Wisconsin (Sass et al., 2021), we tested for abiotic and biotic predictors explaining variability in depensation. Plausible mechanisms or interactions measuring fish community composition and relative abundance, riparian and watershed land cover, and climate were tested for their relative influences on recruitment depensation. We hypothesized that fish community and climate predictors would best explain variation in recruitment depensation. Specifically, we hypothesized that largemouth bass (*Micropterus salmoides*, Centrarchidae) relative abundance and growing degree days would be positively correlated with the probability of depensation given the findings of previous research on walleye recruitment in general (G. J. A. G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Hansen et al., 2018). Using the model that best explained variation in recruitment depensation, we then sought to predict the potential strength of depensation for other walleye populations with insufficient data to directly estimate depensation. To place our results in a management context, we combined depensation estimates with adult walleye density and stocking information to describe where different types of management actions may be most appropriate.

2. Methods

In order to understand potential mechanisms driving depensation in walleye, a series of models containing different potential predictors were fit to the existing depensation estimates published in Sass et al. (2021). The following subsections are ordered such that the analytical method used to address our hypothesis is described first followed by descriptions of both the predictor and response data that was analyzed. Finally, a brief explanation of how the results of our modeling efforts can be applied to the management of this valuable species.

Our analysis was carried out across two sets of lakes. First, an ‘inference’ set consisting of lakes where q had been previously estimated and covariate information was available ($N = 28$). Briefly, q values for 82 Wisconsin walleye populations were originally published in Sass et al. (2021), of which 28 had the necessary covariate data (land cover, climate, adult abundance, fish community, and competitor abundance) to be included in our model selection process (Table 1). These 28 inference lakes were used to identify the model that had the best out-of-set predictive capacity and most parsimoniously explained

Table 1

Candidate factors included in the model selection process and the depensatory mechanism they represent.

Variable Name	Definition	Mechanism
Largemouth Bass CPE	Mean catch per mile of largemouth bass during spring electrofishing surveys of the given lake's shoreline	Cultivation Effect
Fish Community PC1	Principle Coordinate axis 1, variation in the presence/absence of panfish and largemouth bass	Cultivation Effect
Adult Walleye Density	Mean density of adult walleye for a given waterbody	Impaired Group Dynamics Effect
Growing Degree Days	Mean annual growing degree days with a base of 5 °C	Habitat Effect
Riparian Land Cover PC1	Principle component axis 1, variation in wetland and forested land cover at riparian scale	Habitat Effect
Riparian Land Cover PC2	Principle component axis 2, variation in developed land cover at riparian scale	Habitat Effect
Watershed Land Cover PC1	Principle component axis 1, variation in pasture and cultivated land cover at watershed scale	Habitat Effect
Watershed Land Cover PC2	Principle component axis 2, variation in the wetland and forested land cover at watershed scale	Habitat Effect

variation in q across populations. Once the best fitting model was identified, we predicted q values for lakes which contained walleye populations and measurements of the necessary covariates to fit the model but lacked sufficient data to directly quantify q ($N = 115$); hereafter referred to as 'prediction' lakes.

2.1. Analysis

Selecting the best fitting model required assessing the tradeoff between improved model fit to the data and the ability to predict q in lakes where q could not be directly estimated. Given the eight predictors and the potential for interactions among them, the number of candidate models can be calculated as $2^{(8^2)}$ resulting in 2.4×10^{24} unique models. To address our hypothesis dispassionately and efficiently a genetic algorithm was used to identify the subset of models that best explained variation in walleye recruitment in lieu of an exhaustive search of the full set of 2.4×10^{24} unique models. The resulting subset of models were then compared and cross-validated to identify the model to be used for predicting q values for the prediction set of lakes (Fig. 1).

Genetic algorithms have been shown to be very efficient at exploring large sets of candidate models and successful in identifying the key predictors and model structures (Calcagno and de Mazancourt, 2010; Orestes et al., 2009; Trevino and Falciani, 2006). The genetic algorithm (GA) method uses the principles of evolution by natural selection to return a set of models with predictors that are "more fit" as judged by the algorithm using Akaike's Information Criterion for small samples (AICc). The GA begins with a user specified number of models (starting population of models) randomly drawn from the full set of unique models. Each model represents an alternative 'genotype' based on what predictors are included and excluded in relation to the full model where all predictors and interactions are included. Each of the models in the population are fit to the data and the resulting AICc values are stored.

The next 'generation' of models in the population are then proposed with changes in the model genotypes represented in the population evolving through processes termed asexual reproduction, sexual reproduction, and immigration (Fig. 1). Here, asexual reproduction involves directly copying a model from one generation to the next. AICc values are used to weight the probability of a model asexually reproducing such that better fitting models are more likely to be directly passed to the next generation. Sexual reproduction involves the creation of a new model combining two 'parent' models (Fig. 1). As with asexual reproduction, the parents are chosen with probabilities based on their AICc values to create a new model containing the features of both parents. During asexual and sexual reproduction, models can spontaneously mutate at a user-specified rate. This prevents the algorithm from getting mired in local minima by randomly introducing new predictors to the model genotype. As a further check to prevent the GA from failing to find the global minimum in AICc, immigration occurs at each generation to introduce an entirely new, randomly selected model into the population at a rate specified by the user. The algorithm then repeats for hundreds or thousands of generations to refine the population of models by probabilistically selecting for the best models at each step to produce a final population that has 'evolved' towards the global minimum in AICc value. When no further improvements in AICc can be achieved for a specified number of generations, the algorithm stops and the final population of models is returned. This population represents the set of model structures determined to best fit the data by the GA.

We replicated the GA process 20 times to ensure that the GA had fully searched the entire candidate set of models and located the global minimum in AICc regardless of the starting model populations (Fig. 1, Calcagno and de Mazancourt, 2010). A consensus population of models was then created by selecting the top 100 models from across the 20 unique GA runs to ensure that all the top performing models from each run were included in the consensus set of models (Appendix A: Fig. A.1).

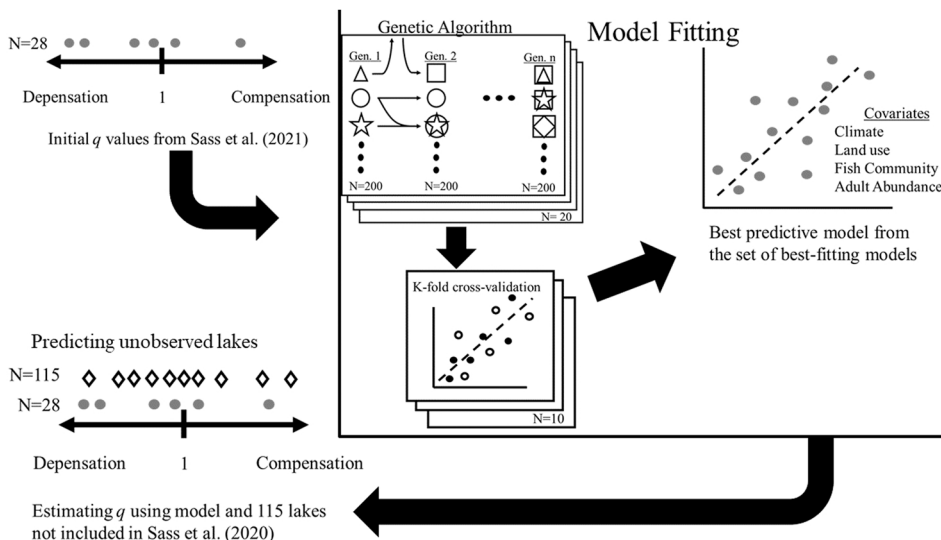


Fig. 1. Conceptual diagram of the analysis beginning in the upper left corner with the original depensation risk (q) values published in Sass et al. (2021). The process of fitting and validating the model to the data from Sass et al. (2021) is described in the 'model fitting' box. Briefly, a genetic algorithm is used to efficiently search the large set of potential models and find the best fitting model by allowing a population of models ($N = 200$) to evolve over time towards the best fitting model. This process is repeated 20 times to identify a set of best fitting models. The resulting set of models is then evaluated for their ability to predict out-of-set using k-fold cross validation; this is repeated 10 times and the model with the best ability to predict out of set is chosen. This results in a model that can be applied to 115 additional lakes to predict their q values, which can then be combined with the values from Sass et al. (2021) for further analysis (bottom left corner).

From this consensus population of models, the model with the lowest AICc value was identified and all models within 2 AICc values of the lowest AICc model were chosen for cross-validation to assess their ability to predict out of sample. Three models fell within this threshold. These models were k-fold cross-validated ($k = 5$), where the inference set of lakes was randomly split into 5 groups and each of the 4 models (lowest AICc model plus the three within 2 AICc values of it) chosen for cross-validation was fit to a data set containing 4 out of 5 groups of the inference data. The left-out group of data was then predicted using the resulting model fit from the combined 4 groups. Each of the 5 subsets of the data set were iteratively held out and predicted for each of the 4 cross-validation models. The k-fold cross-validation was repeated 10 times for each model to ensure that the random splitting of the data into 5 groups did not inadvertently bias our assessment of each model's ability to predict the held-out data (Fig. 1). The ability of each model to predict the held-out data was assessed using the root-mean-squared-error comparing the model prediction of the held-out data to the actual values. Lower root-mean-squared-error signified a better predictive ability of the model.

2.2. Response data set

We quantified recruitment depensation using the parameter q developed by Liermann and Hilborn (1997), which describes the predicted magnitude of the density-dependent response at low population size, where $q < 1$ suggests evidence for depensatory recruitment and $q > 1$ suggests evidence for compensatory recruitment. The metric q is the ratio of recruitment predicted at 10% of the maximum observed spawner abundance from the standard Beverton-Holt stock recruitment model and a version allowing for depensation, and is theoretically bounded between 0 and 1.55 (Appendix A 1.4, Liermann and Hilborn, 1997).

2.3. Predictor data set

Potential covariates for the depensation model were selected from a suite of abiotic and biotic data covering lakes with walleye populations across Wisconsin and are summarized in Table 1 and more fully described in Appendix A 1 as well as G. J. A. Hansen et al. (2015); J.F. Hansen et al. (2015) and Winslow et al. (2017). To test our hypothesis about drivers of depensation in walleye, we developed a set of eight environmental covariates representing different plausible mechanisms that may influence the probability of recruitment depensation, which we describe in the sections below (Table 1; Appendix A 1).

2.3.1. Cultivation effects

Fish community composition may play an important role in walleye recruitment, with the presence or absence of key predators, competitors, or prey species that can cultivate conditions for themselves and negatively influence walleye recruitment. Consequently, we used presence/absence data of ten fish species and species complexes (Appendix A 1.1). To control for collinearity between the presence/absence of different fishes a principal coordinates analysis (PCoA) based on a Sørensen's distance matrix was used to summarize variation in fish community composition. Only the first axis was considered as a potential predictor because it accounted for the bulk (86%) of the variation in the data. PCo1, which was included as a candidate predictor, represented variation in panfish and largemouth bass presence/absence, which were positively correlated (Appendix A Table A.5). If fish community composition is an important driver of depensation, the key axis of variation described by our PCoA should be chosen in our variable selection process as a predictor of q that significantly improves model fit (Table 1).

Largemouth bass are a key species thought to influence walleye recruitment and represent a feasible path towards depensation through the inability of walleye to condition their environment or the increased

ability of largemouth bass to cultivate favorable conditions for themselves (Fayram et al., 2005; Grausgruber and Weber, 2020, 2021a; Hansen et al., 2015, 2018; G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Lyons and Magnuson, 1987; Santucci and Wahl, 1993; Sullivan et al., 2020, but see Embke et al., 2022; Kelling et al., 2016). In this case abundant adult walleye prevent largemouth bass from becoming abundant through foraging effects and when walleye abundance is reduced, by angler harvest for example, a window of opportunity is opened for largemouth bass to increase in abundance. With the alleviation of foraging effects by walleye, largemouth bass become abundant and their own foraging habits in turn prevent walleye from reestablishing their dominance. Largemouth bass relative abundance estimates were included to test the hypothesis that depensation may occur through an absence of conditioning of the environment by walleye (i.e., 'cultivation' effects of largemouth bass, Appendix A 1.1). Should largemouth bass cultivation effects be important drivers of walleye depensation, q values would be expected to be negatively correlated with largemouth bass CPE.

2.3.2. Impaired group dynamics

Consequently, depensatory recruitment effects could occur through impaired group dynamics leading to reduced feeding efficiency as abundance declines. Reduced feeding efficiency can in turn lead to reduced body condition, which has been shown to influence recruitment of walleye (Feiner et al., 2019, 2016; Shaw et al., 2018). If this mechanism is an important driver of depensation, adult walleye density would likely be a significant predictor of recruitment depensation (further detail on the collection and processing of adult abundance data can be found in Appendix A 1.2). In practice, this would mean that adult walleye density would be positively correlated with q such that depensation would be less likely (i.e., higher q values) when mean adult densities were higher. It stands to reason that adult density may influence recruitment in other ways than impaired group dynamics (i.e. mate scarcity, conditioning effects), and should average adult density be included in the best fitting model it may be difficult to distinguish between potential mechanisms linking q to average adult density.

2.3.3. Land cover and physical habitat effects

Abiotic variables have been shown to influence walleye recruitment in general including land cover and water temperature. Land cover predictors were included because of their influences on walleye habitat and lake productivity (Appendix A 1.3), which could contribute to depensation by altering available prey and physical and thermal-optical habitat needed by walleye for foraging and reproduction (Lester et al., 2004; Bozek et al., 2011; Raabe et al., 2020). The negative effects of these factors on recruitment may also impact the risk of depensation in a particular population by altering the critical abundance threshold for depensation or magnifying the effects of density-dependent factors like predator abundance.

A variety of land cover metrics were used to capture abiotic variables likely to influence walleye recruitment. Land cover data at the riparian (within 100 m of water's edge) and watershed scale described the proportion of the land comprised of forest, shrubs, grassland, pasture, cultivated, wetland, developed, and barren land cover. To control for significant correlation among land cover variables, we conducted a Principal Components Analysis (PCA) to reduce the high-dimensional data to two orthogonal axes for watershed and riparian land cover, each (Table 1). Results of the PCA for the watershed land cover information described land cover at the watershed scale to be positively correlated with pasture and cultivated land along the first axis. The second axis was positively correlated with forest and negatively correlated with wetland (Appendix A: Table A.3, Fig. A.2). Together, these axes explained 90% of the variation in watershed land cover. At the riparian scale, the first riparian PCA axis correlated negatively with forest and positively with wetland land cover. The second axis was correlated negatively with developed land cover (Appendix A: Table A.4

Table 2

Model terms and coefficient estimates for the best predictive model from the genetic algorithm and cross-validation.

Coefficient	Estimate	Std. Error	p-value
Intercept	9.62×10^{-1}	6.77×10^{-2}	1.45×10^{-12}
BassCPE [†] :degreedays5 [‡]	-2.49×10^{-5}	9.20×10^{-6}	0.013
BassCPE: fishcommPC1 [§]	2.89×10^{-1}	9.76×10^{-2}	0.007
BassCPE: riparianPC1 [¶]	5.78×10^{-1}	1.66×10^{-1}	0.002
BassCPE: watershedPC2 ^{††}	-4.62×10^{-1}	2.36×10^{-1}	0.064
RiparianPC1:fishcommPC1	-4.76	1.70	0.010

[†]BassCPE= log of the largemouth bass catch per km[‡]degreedays5 =growing degree days at 5 °C[§]fishcommPC1 =fish community PCoA axis 1[¶]riparianPC1 =riparian PCA axis 1^{††}watershedPC2 =watershed PCA axis 2

and Fig. A.3). Together, these axes explained 91% of the variation in riparian land cover.

Warming temperatures are predicted to negatively influence walleye recruitment in some lakes (Hansen et al., 2017; Rypel et al., 2018). We included lake-specific mean annual growing degree days at 5 °C during 1980–2015 as candidate predictors to test for climate influences. These data are the result of large spatial extent modeling efforts by the USGS and are freely available as referenced in Winslow et al. (2017).

2.4. Framing model output in a management context

The predictions of q provided by the best model are most useful, from a manager's perspective, when viewed through the lenses of average adult walleye density and walleye stocking history. This provides managers with some perspective as to the status of a given walleye population, via its stocking history and adult density, and the likelihood of future management action paying off should population sizes decline, via its q value. Plotting predicted q values against average adult walleye density is one example of how the model output can be analyzed with a management application focus. In this case, lakes with strong depensation and low abundances may exhibit the weakest response to conservative management efforts, while lakes with low adult abundance and strong compensatory recruitment may show stronger responses. Similarly, stocking, which is common throughout the state as a tool to prevent or rehabilitate population declines, is a key piece of context managers want and is therefore relevant to applying our model results to management (Feiner et al., 2022; Hansen et al., 2018; Sass et al., 2022; Shultz et al., 2022). Viewing our results through a stocking lens can help managers see how limited stocking resources are being applied across compensatory and depensatory populations and whether they should be allocated differently.

Non-parametric analysis of variance tests (Mann-Whitney U and Kolmogorov-Smirnov) were used to compare different lake groups based on their q values and stocking rates to test whether stocking practices were significantly different in compensatory ($q > 1$) vs. depensatory ($q < 1$) lakes. Specifically, the mean biomass of stocked walleye/m² for a given lake was compared between compensatory and depensatory lakes. Because mean stocked walleye biomass was not normally distributed, we used a Kolmogorov-Smirnov test to perform this comparison (null hypothesis of no difference between groups, $\alpha = 0.05$). Additionally, the q values for lakes with and without stocking histories were also compared to test whether stocked lakes were more likely to be lakes with depensatory q values than non-stocked lakes. Again, the distributions of q values for stocked and non-stocked lakes did not meet the assumptions of normality. As a result, a Mann-Whitney U test was used to make this comparison (null hypothesis of no difference between groups, $\alpha = 0.05$).

3. Results

Depensatory recruitment was a more common risk for walleye populations than previously thought (Sass et al., 2021), and the relative

abundance of largemouth bass played a central role in determining the risk of depensation in walleye populations. The final model predicting depensation included five interactions among predictor variables – largemouth bass CPE was included in four of these terms (Table 2). Fish community PCo1 (panfish/largemouth bass presence), riparian land cover PC1 (forest and wetlands), watershed land cover PC2 (forest and wetlands), and growing degree days (5 °C) all interacted with largemouth bass CPE. The largemouth bass interaction with growing degree days had a negative relationship with q values, where more depensatory values occurred with higher largemouth bass CPE and higher growing degree days. The interaction between largemouth bass CPE and riparian land cover and watershed land cover followed the same pattern, where riparian and watershed land cover represented an effect of forest and wetland land cover on walleye depensation when largemouth bass were relatively rare (Table 2). When largemouth bass CPE was low, PC values at riparian and watershed scales spanned the range from wetland-dominated to forest-dominated and q values were compensatory for both land cover types. As largemouth bass CPE increased, PC values concentrated around intermediate values, signaling a mixture of forest and wetland riparian land cover, and q values tended to be more depensatory. Overall, when largemouth bass were relatively more abundant, the importance of land cover diminished, and q values became more depensatory. The largemouth bass interaction with fish community PCo1 followed a similar pattern to the largemouth bass-growing degree days interaction. Depensatory q values occurred in systems with more largemouth bass and where panfish were present, while compensatory q values could occur when panfish were either present or absent, so long as largemouth bass were rare. The sole model coefficient that did not contain a largemouth bass CPE effect specifically was the interaction between riparian PC1 and fish community PC1, where depensatory q values were associated with forested systems likely to have panfish/largemouth bass. Compensatory lakes were those less likely to have panfish/largemouth bass, with little effect of riparian land cover. Importantly, average adult walleye density was not included in any of the top 5 models returned by the GA for cross-validation (Appendix A Table A.1).

Across the 10 k-fold cross-validation runs, the final model had an average root-mean-squared-error of about 0.26, which was the lowest of the top five models tested (Appendix A: Table A.1). When predicting the held-out data, the model generally performed well with only 5 out of 28 lakes being predicted incorrectly (i.e., a depensatory lake being predicted to be compensatory by the model or vice versa) (Fig. 2). The majority (23/28 or 82%) of lakes were correctly predicted to be depensatory or compensatory by the model when compared to the q values presented in Sass et al. (2021). The model tended to provide more conservative estimates of q than were reported for the same lakes in Sass et al. (2021), meaning that for extreme depensatory or compensatory q values, the model predicted more conservative q values (Fig. 2).

Predicted q values signaled potential recruitment depensation in many prediction lakes (73 out of 115) (Fig. 3). Even when accounting for prediction uncertainty, 50 of the 115 lakes had q estimates with 95% CI

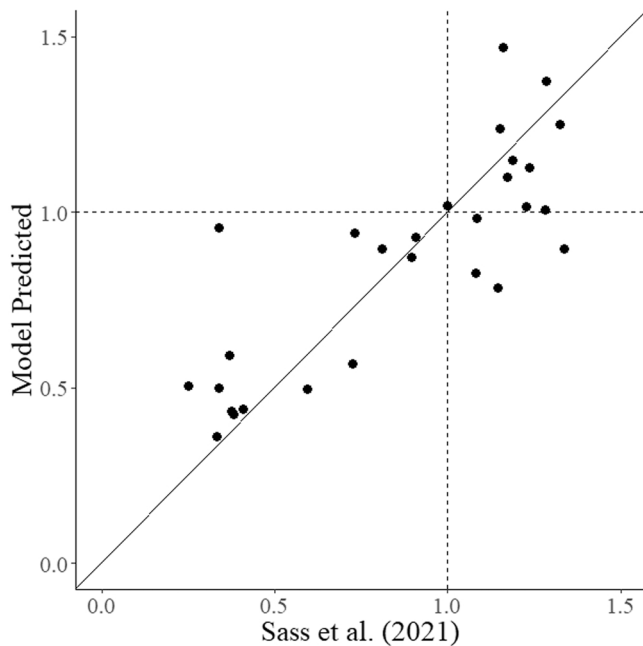


Fig. 2. Sass et al. (2021) vs. model predicted depensation risk (q) values for the 28 inference lakes using the best fitting model in relation to a 1:1 line (solid black line) representing perfect prediction. Horizontal and vertical dotted lines note separation between compensation (to the left/above) and depensation (to the right/below) for each axis. Fifteen lakes with depensatory q values from Sass et al. (2021) were correctly predicted to be depensatory by the model. Nine lakes with compensatory q values from Sass et al. (2021) were correctly predicted to be compensatory by the model. One lake with a depensatory q value from Sass et al. (2021) was predicted to be compensatory by the model. Four lakes with compensatory q values from Sass et al. (2021) were predicted to be depensatory by the model.

< 1 suggesting strongly depensatory recruitment. Nine lakes had q estimates with 95% CI > 1 , signaling strong compensatory recruitment at low population size (Fig. 3). Uncertainty around point estimates of q meant that 56 of 115 prediction lakes had 95% CI overlapping 1, signaling neither strong compensation nor depensation occurring at low population size (Fig. 3). Eight lakes had q estimates or confidence intervals that exceeded the theoretical upper limit of 1.55 and two exceeded the lower limit of 0 (Fig. 3).

Using q values and average adult walleye density, populations can be classified for management priority according to their average adult densities and strength of depensation. Across the “inference” and “predicted” lake data sets, there were 143 lakes with estimates of adult walleye density and q . Of these, 55 populations had point estimates of $q \geq 1$ suggesting compensatory recruitment at low population size, and 45 of those populations had average adult densities below the “sustainable” threshold (7.4 adults/ha, Fig. 4); making them promising targets for stock rehabilitation. However, the majority ($n = 88$) of walleye populations across “inference” and “predicted” lakes fell into the depensatory region. Of these depensatory lakes, 17 populations had adult densities above the “sustainable” threshold and were likely good candidates for maintaining sufficient densities to avoid depensatory recruitment dynamics at low population size. The remaining 71 populations had q values < 1 , adult densities below the sustainable threshold, and thus were the most likely to be affected by depensatory recruitment given their already low adult abundances.

Stocking was equally likely across compensatory and depensatory lakes, with no significant difference in stocking rate for compensatory and depensatory lakes. Across the “inference” and “predicted” lake set, 137 lakes were stocked and 9 were not. Stocking rates did not differ between predicted compensatory and depensatory lakes (Kolmogorov-

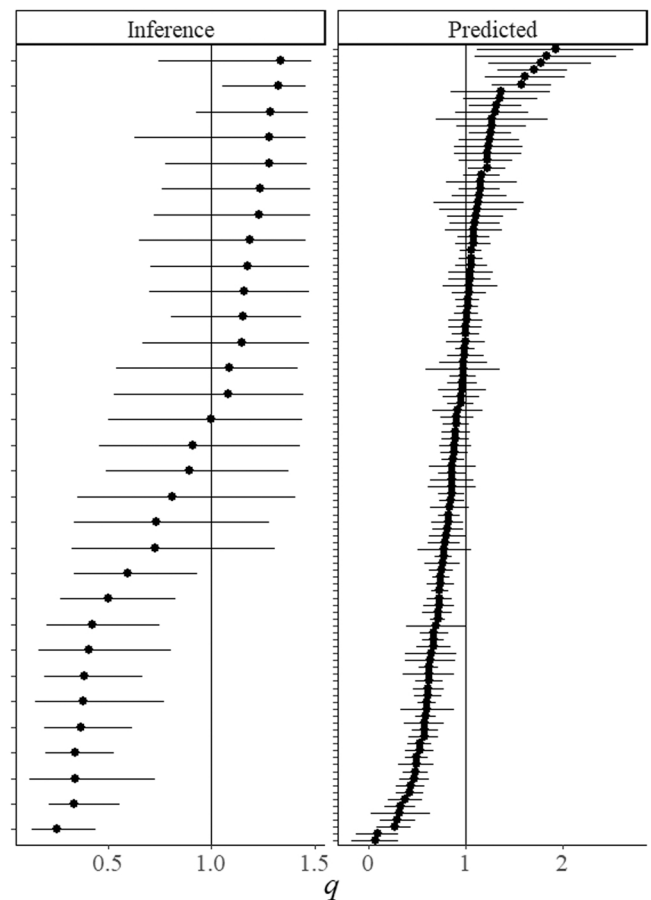


Fig. 3. Lake-specific estimates of depensation risk (q) for the inference and predicted lake sets. Vertical black line notes separation between depensation (to the left) and compensation (to the right). Horizontal black lines through each point estimate of q are 95% credible intervals from the original Sass et al. (2021) Bayesian posterior distributions of q (inference column) and the 95% confidence intervals from the bootstrapping of modeled q values (predicted column).

Smirnov test $p = 0.650$; Fig. 5a). Between the groups of stocked and non-stocked lakes, q values did not differ (Mann-Whitney U test $p = 0.371$; Fig. 5b).

4. Discussion

Depensation poses a significant risk to fish populations that have been severely reduced through harvest or other interacting factors (Carpenter et al., 2017; Embke et al., 2019; Post et al., 2002; Sass et al., 2021, 2017; Walters and Kitchell, 2001). Despite the common assumption of compensatory recruitment facilitating recovery when population size is reduced, there is growing evidence that reductions in population size below a critical threshold can lead to reductions in recruitment and further population decline (Hutchings, 2014). We modeled variation along a compensation/depensation gradient for 28 walleye populations (“inference” set of lakes), with measures for eight potential biotic and abiotic predictors. Our model selection process identified the interactions between largemouth bass CPE and growing degree days, presence/absence of panfish species, and the prevalence of forested and wetland land cover at the riparian and watershed scale as important factors predicting depensatory recruitment dynamics. Using this model, we then predicted q values for 115 additional walleye populations (“prediction” set of lakes). We found that 43% of the prediction lakes could be vulnerable to depensatory recruitment at low population size given their biotic and abiotic lake characteristics.

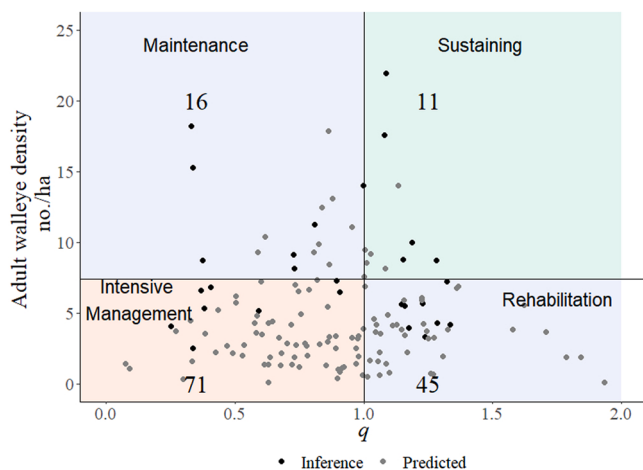


Fig. 4. Mean adult walleye density (no./ha) associated with depensation risk (q). Horizontal black line represents minimum 7.4 adults/hectare defined by U. S. Department of the Interior as a ‘quality’ walleye population. Vertical black line is separation between depensation (to the left) and compensation (to the right). The number of lakes in each quadrant of the plot are noted on the plot. Shaded quadrants correspond to walleye populations that may need some management assistance to maintain good density (Maintenance) or recover (Rehabilitation), little management assistance (Sustaining), or high amounts of assistance (Intensive Management) to the point where the long-term future of those populations could be reconsidered.

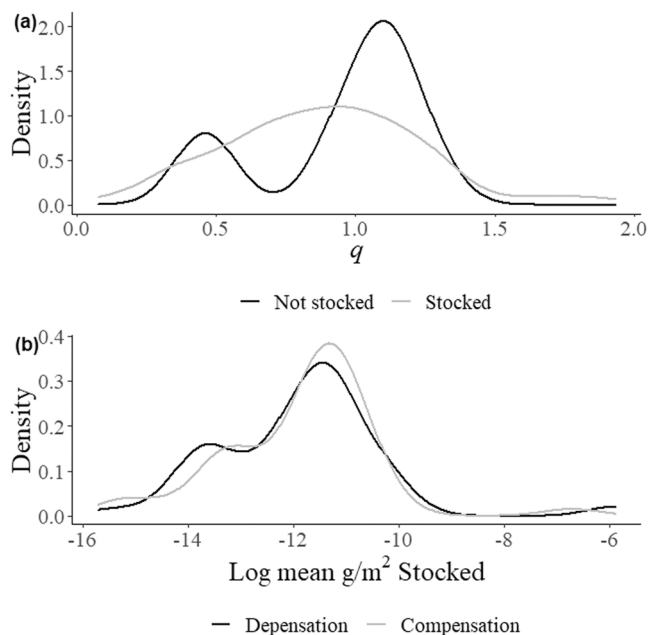


Fig. 5. (a) Distribution of depensation risk (q) for stocked and not stocked lakes across all inference and predicted lakes. There was no significant difference between q values for stocked and not stocked lakes across all inference and predicted lakes (Mann-Whitney U test $p = 0.371$). (b) Distribution of walleye biomass stocking rates for compensatory and depensatory lakes across all inference and predicted sets of lakes. There was no significant difference between stocking rates for compensatory and depensatory lakes (Kolmogorov-Smirnov test $p = 0.650$).

4.1. Mechanisms of depensation

The interaction between largemouth bass CPE and several other predictors further supports the previously noted negative interactions between largemouth bass, or centrarchids in general, and walleye recruitment (Broda et al., 2022; Embke et al., 2022; Hansen et al., 2018;

G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Kelling et al., 2016; Sullivan et al., 2020). Climate change, land cover, and centrarchids (particularly largemouth bass, black crappie, white crappie *Pomoxis annularis*, Centrarchidae) have all been described separately as factors influencing natural recruitment in walleye (J. F. G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Hansen et al., 2017; Rypel et al., 2018; Bozek et al., 2011; Raabe et al., 2020; Quist, Guy, and Stephen, 2003; Broda et al., 2022, but see Hansen et al., 2018 for a notable exception). Here, we focused specifically on recruitment at low abundances where depensation can occur. Although all the covariates described here have been shown by others to influence walleye recruitment, none have focused specifically on recruitment at low population sizes. For example, warming water temperatures because of climate change influence walleye recruitment regardless of adult density, while other factors like largemouth bass CPE may only have an influence when walleye densities are low and thus more sensitive to losses from predation or potential competition. Furthermore, the consistent interaction between various abiotic (growing degree days, riparian and watershed scale land cover) and biotic (panfish presence/absence) lake characteristics and largemouth bass CPE have not always been observed in other studies of walleye recruitment in general (Hansen et al., 2022). The widespread effect of largemouth bass here points towards the critical role this species may have on walleye recruitment dynamics at low population size. Similarly, the inclusion of an interaction effect between riparian land use and panfish/largemouth bass presence in the model also points towards potential conditioning effects via fish community composition. These effects appear to support the notion that largemouth bass (and perhaps centrarchid panfish), may be conditioning the environment in their favor at the expense of walleye.

If largemouth bass play a critically important role in regulating walleye recruitment at low abundances, as our results suggest, this is most likely achieved through their ability to condition the environment (i.e., cultivation effects) to favor their own success. Similar cultivation effects have been observed in many taxa (Liermann and Hilborn, 2001; Myers et al., 1995; Stamou and Asikidis, 1989; Van Leeuwen et al., 2008; Walters and Kitchell, 2001). In the case of walleye and largemouth bass, these cultivation effects are likely achieved through competition for shared prey resources and may also include direct predation of largemouth bass on walleye as previous work has suggested (Fayram et al., 2005; Grausgruber and Weber, 2020; Kelling et al., 2016; Santucci and Wahl, 1993). Several studies have noted a negative correlation between largemouth bass CPE and walleye abundance (Hansen et al., 2018; G.J. A. Hansen et al., 2015; J.F. Hansen et al., 2015; Inskip and Magnuson, 1983; Nate et al., 2003), and these interactions may be asymmetrically advantageous for largemouth bass. As just one example, Fayram et al. (2005) noted that largemouth bass diets overlapped more with juvenile walleye than adult walleye, and that walleye comprised a greater percentage of largemouth bass diets than largemouth bass comprised of walleye diets. Our results provide another line of evidence among a growing list of studies that suggest walleye recruitment is in part controlled by the ability of adult walleye to cultivate favorable conditions for their offspring. When walleye are unable to do so, other species like largemouth bass gain a window of opportunity where predation/competition with walleye is alleviated and their abundances increase. Increasing largemouth bass abundances allow them to begin structuring the ecosystem to their own benefit at the expense of walleye. This flip in dominant species from walleye to largemouth bass likely contributes to the inability of some walleye populations to recover from low abundances (Shultz et al., 2022).

Given that cultivation by other species, namely largemouth bass, appears to be a major determinant of which walleye populations experience depensatory recruitment at low adult densities, there may be other species that should be considered. For example, bullheads (*Ameiurus* spp.) and crappies (*Pomoxis* spp.), when abundant, have been shown to negatively influence walleye recruitment in a handful of systems. In northern Wisconsin lakes, experimental removals of highly

abundant black (*A. melas*, Ictaluridae) and yellow (*A. natalis*, Ictaluridae) bullheads resulted in increased walleye recruitment and adult abundances (Sikora et al., 2021). Similar negative interactions have been observed between crappies and walleye recruitment, which were also a component of the panfish fish community covariate included in our model. While our model does point to the presence of panfish (which include crappies) as an important component explaining variation in depensation, standardized sampling of crappie relative abundances does not exist yet on a statewide scale in the same way that largemouth bass CPE is sampled. Thus, we are currently unable to fully evaluate the impact of crappie relative abundance on depensation as was done for largemouth bass. Still, Quist et al. (2003) found a strong, negative relationship between walleye recruitment and white crappie (*Pomoxis annularis*, Centrarchidae), with predation of young-of-the-year walleye by white crappie as the most plausible driver. A similar relationship was observed between walleye recruitment and black crappie in Wisconsin lakes (Broda et al., 2022). However, because crappies and bullheads are not surveyed in a standardized way on a statewide scale, relative abundance data does not exist for these species in our set of lakes. Further effort to characterize bullhead and crappie relative abundances at state and regional scales could provide additional insight into walleye recruitment dynamics in the same way that largemouth bass relative abundance has here. Given the documented declines in walleye populations throughout the state (Embke et al., 2019; Pederson et al., 2017; Rypel et al., 2018) and the role certain species like largemouth bass, crappies, and bullheads may play in walleye recruitment dynamics, a better understanding of these biological factors may provide managers with additional tools to rehabilitate and maintain walleye populations into the future.

In addition to the potential cultivation effects of centrarchids (e.g., largemouth bass) deleteriously influencing walleye recruitment, anthropogenic influences in the form of climate change and angler behavior have also positively influenced largemouth bass populations, potentially at the expense of walleye. Human-mediated climate change, through increased water temperatures, indirectly tilts the competitive scales in favor of warm-water species like largemouth bass, while cool-water species like walleye are disadvantaged (Feiner et al., 2022). Hansen et al. (2018) described variation in successful walleye natural recruitment as best explained by an overall climate warming effect (measured as growing degree days) modified by lake surface area and largemouth bass CPE. Concurrent with more favorable water temperatures, relative abundance of largemouth bass has also benefitted from changes in human behavior independent of changes in climate. Specifically, a combination of conservative regulations, protection during the spring spawning season, and voluntary release of largemouth bass by anglers has promoted black bass abundance increases alongside favorable climate conditions (Gaeta et al., 2013; G.J.A. Hansen et al., 2015; J. F. Hansen et al., 2015; Miranda et al., 2017; Rypel, 2015; Rypel et al., 2016; Sass et al., 2021, 2018; Sass and Shaw, 2020). The changing angler preference to release largemouth bass, while still maintaining harvest of walleye, further promotes increases in largemouth bass in lieu of walleye. Interestingly, a recent whole-lake removal of centrarchid species, testing the hypothesis that intense centrarchid management may positively influence walleye recruitment, showed no short-term improvements in walleye recruitment compared to pre-removal and control lake data (Embke et al., 2022). However, largemouth bass were not removed in high enough numbers to significantly change their abundance, leaving their direct influence on walleye recruitment somewhat unclear. Taken together, warming water temperatures and high voluntary release rates for largemouth bass are likely working against walleye, while pointing towards improving conditions for centrarchids like largemouth bass.

4.2. Management context

Predictions of q suggested that many walleye populations in our

study lakes showed the potential for depensatory recruitment dynamics, which can hasten population declines that are already being observed for many walleye populations and reduce their response to rehabilitation efforts (Embke et al., 2019; Feiner et al., 2022; Pederson et al., 2017; Rypel et al., 2018; Shultz et al., 2022). For example, the proportion of CTWI walleye populations solely supported by natural recruitment has significantly declined over time suggesting that depensation has occurred and is likely to continue according to our results (Rypel et al., 2018; Sass et al., 2021). This is not to say that most lakes are actively undergoing depensatory recruitment. Instead, largemouth bass CPE in each of these lakes, in addition to the other lake characteristics identified in our model, suggest that depensatory recruitment is predicted to occur should populations decline. Even when accounting for uncertainty around estimations of q using our model, nearly half of the prediction lakes had q values and 95% CI intervals < 1 suggesting depensation is likely should abundances decline in these lakes (Fig. 3). Of the remaining lakes, almost all had confidence intervals overlapping 1, suggesting neither a strong compensatory nor depensatory response at low population size (Fig. 3). In total, the preponderance of evidence from our models suggested either density-independent or depensatory recruitment in walleye populations at low densities. Contrary to most management strategies and fisheries models, which rely on compensatory recruitment to allow populations to rebuild themselves, density-independent and depensatory recruitment responses at low abundances limit the ability of walleye populations to replenish themselves through natural recruitment or to respond strongly to typical management tools (i.e., stocking, conservative harvest regulations, fishery closure). This may be true for other fish species, but generally the data to assess stock-recruitment relationships generally and at low stock size is lacking for most freshwater species. Importantly here, the walleye fishery is co-managed by state, federal, and tribal entities leading to a relatively data-rich system compared to other species. Changing environmental condition, high harvest, failing recruitment, and a guild of warmwater species, including some that are only lightly harvested, ready to replace walleye are all creating an uphill battle for this valuable species. Our results, along with the interactions between largemouth bass CPE and climate in other studies on walleye recruitment, point toward declining quality and quantity of walleye populations for this region (Dassow et al., 2022; Feiner et al., 2022; Hansen et al., 2018, 2017; G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Rypel et al., 2018; Shultz et al., 2022).

An understanding of the strength of recruitment depensation for a given population can be used to inform management strategies for conservation, enhancement, or acceptance and transition to an alternative fishery (Lynch et al., 2021; Schuurman et al., 2021). These strategies are encapsulated in the Resist-Accept-Direct (RAD) framework where the three categories describe management actions based on whether they seek to maintain the ecosystem service in the face of change (resist), accept the change and the new ecosystem dynamics it brings (accept), or accept the change and take some actions to direct the system towards a more desirable new state (direct; Schuurman et al., 2021; Thompson et al., 2021). Furthermore, our results suggest that managers will need to consider the biotic and abiotic characteristics of individual lakes as they work to identify which walleye populations should be prioritized for conservation over others (Dassow et al., 2022; Rypel et al., 2019; Tingley et al., 2019). According to our results and previously published research on climate effects (G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Hansen et al., 2017; Rypel et al., 2018), the walleye populations likely to persist into the future are those with low relative abundances of largemouth bass and consistently cooler water temperatures. A “sustainable” walleye population in the CTWI is defined as containing ≥ 7.4 adults/ha (U.S. Department of the Interior, 1991). Those systems above the “sustainable” threshold and with compensatory q values are likely to be some of the most resilient populations. These systems are good candidates for continued monitoring, and unlikely to need management intervention in the short-term, in the

RAD framework, these are likely to be good systems for resist-oriented actions. Compensatory lakes below the “sustainable” threshold are likely good sites for minor management action. Their q values suggest that abundances should be able to rebound from low population sizes and could provide positive results from minimal effort, again positioning them well for resist-oriented actions. Depensatory lakes above the “sustainable” threshold are unlikely to rebound should population size decline and are unlikely to provide a good return on investment for rehabilitation efforts. Nevertheless, they are good candidates for preventative actions to maintain higher adult densities. For these lakes, emphasizing proactive, resist-oriented, measures could be a good strategy to maintaining these populations. Lastly, depensatory populations already below the “sustainable” threshold may be poor investments of limited management resources aimed at resisting walleye declines given their likelihood of depensation and already compromised populations. These populations will be better suited for accept or direct strategies within the RAD framework.

Stocking is the most common management intervention used in attempts to increase walleye abundances and to rehabilitate natural recruitment, but our results suggest it may not be deployed as effectively as it could be. An analysis of stocking occurrences and rates related to our q values showed that the decision to stock and the stocking rate did not differ between compensatory and depensatory systems (Fig. 5). Given that compensatory and depensatory lakes are stocked equally, in terms of the decision to stock and the stocking rate, the q values presented here suggest that many of those stocked, depensatory systems are unlikely to respond to this pervasive management action. Over time, stocking of extended growth walleye fingerlings (177–203 mm TL) has been preferred over fry and small fingerlings under the assumption of higher survival and a greater probability of restoring natural recruitment. Nevertheless, transport, extended rearing, transitioning to wild prey, and sex ratios skewed towards females have challenged these assumptions (Graumgruber and Weber, 2021b, 2021c; Sass et al., 2021). The role of inter-specific interactions through ‘conditioning of the environment’ effects suggested for depensatory systems here may indicate that stocking is not an effective strategy for rehabilitating walleye populations despite its widespread use (Raabe et al., 2020; Sass et al., 2021, 2017; Shultz et al., 2022). If largemouth bass cultivation plays a key role in depensatory recruitment of walleye, stocking walleye may prove ineffective in some depensatory systems as largemouth bass may benefit from increased foraging opportunities on stocked walleye. Fayram et al. (2005) and Graumgruber and Weber (2020) found evidence of increased occurrence of walleye in largemouth bass diets after stocking events. These findings, and those of Santucci and Wahl (1993), point towards stocking longer (>150 mm TL) walleye as a means of reducing predation risk and increasing survival. This strategy is already being adopted in Wisconsin where some stocking events use fish > 150 mm TL, and 8.3% of stocking events during 2002–2017 used fish longer than 200 mm TL. However, initial returns on investment for stocking longer walleye to rehabilitate natural recruitment have not been promising (B. Elwer, Wisconsin Department of Natural Resources, unpublished data; Lawson et al., 2022). Given our results, and the current knowledge on investment for stocking longer walleye, stocking may be most effective if judiciously applied to lakes where the likelihood of depensatory recruitment is low or where there is no strong indication of depensatory or compensatory dynamics (i.e. lakes with q values near 1). Furthermore, the continued stocking of compensatory systems may be an inefficient use of stocking resources as the evidence for compensatory recruitment in these systems would suggest they are capable of naturally replenishing themselves.

4.3. Conclusion

The strongest factor influencing depensation in our model, largemouth bass CPE, is also potentially the most useful result for managing walleye fisheries. Compared to climate and land cover factors also

affecting walleye recruitment, largemouth bass CPE might reasonably be influenced by a manager seeking to maintain walleye. Nevertheless, this factor would also require a shift in angler attitudes related to largemouth bass. There are multiple avenues for reducing largemouth bass abundances available to managers, the most efficient and long-term solution would be the promotion of increased angler harvest of largemouth bass through liberalization of harvest regulations and a change in social norms by bass anglers to harvest more bass for consumption (Sass and Shaw, 2020). Voluntary catch-and-release of largemouth bass by anglers has become the social norm and this attitude would have to shift to selective harvest in order for liberal harvest regulations to be effective (G.J.A. Hansen et al., 2015; J.F. Hansen et al., 2015; Miranda et al., 2017; Sass and Shaw, 2020; Sullivan et al., 2020). Additionally, largemouth bass are often protected during their spring spawning period in much of the region (i.e., through catch-and-release only or closed fishing seasons) despite no strong evidence for negative population-level influences as a result of nest fishing (Allen et al., 2011; Jackson et al., 2015; Sass and Shaw, 2020). Broad-scale, physical removals of largemouth bass by agencies are time-consuming, costly, often infeasible, and should not be considered a viable walleye rehabilitation strategy (Embeke et al., 2022). Given the relative control regional decision-makers have over largemouth bass abundances compared to climate and land cover change, measured increases in selective harvest of largemouth bass via liberalized regulations and angler outreach should be strongly encouraged when angler and tribal dispositions favor walleye fisheries. Conversely, the warming climate and changing land cover cannot be directly influenced by fisheries managers (Carpenter et al., 2017; Sass et al., 2017), yet these factors play an important role in walleye recruitment. Consequently, managers are left needing to creatively leverage the things they can control, such as the relative abundance of key competitors like largemouth bass, to keep walleye populations in a safe-operating-space despite the effects of factors outside a manager’s control like climate and land cover (Carpenter et al., 2017). Based on our results, conserving walleye populations subject to depensatory recruitment dynamics would be better served by increased angler harvest of largemouth bass and within-lake and watershed management, while placing less emphasis on stocking. Changing the social norm of nearly exclusive voluntary release for largemouth bass among most anglers to selective harvest and watershed-level land cover conservation is of utmost priority where sustainable walleye fisheries are desired.

CRedit authorship contribution statement

Colin Dassow: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing – original draft, Writing – review & editing. **Greg Sass:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Stephanie Shaw:** Data curation, Writing – review & editing. **Zach Feiner:** Formal analysis, Data curation, Writing – review & editing. **Chelsey Nieman:** Conceptualization, Writing – review & editing. **Stuart Jones:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

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.

Data availability

Data from Sass et al. (2021) are available at the publication’s DOI here. The code and data used here will be permanently stored at the following link if accepted (https://github.com/cdassow/Cultivation-Depensation_Manuscript.git).

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