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Linking fish population dynamics to habitat conditions: insights from the application of a process-oriented approach to multiple species

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Introduction

The Strategic Great Lakes Fisheries Management Plan Joint Strategic Plan (GLFC 1997) is a central guide for fisheries management of the Laurentian Great Lakes. The Joint Strategic Plan (JSP) led to the creation of Lake Committees which comprise representatives of the fisheries management agencies with jurisdiction over each of the five Great Lakes. First among the charges to these Lake Committees in the JSP is that each committee should "define objectives for the structure of each of the Great Lakes fish communities" (GLFC 1994, p. 11). These fish community objectives are intended to guide fisheries management decision-making by providing targets against which fisheries management performance can be measured. At the same time, the JSP led to the creation of the Habitat Advisory Board, whose central purpose was to facilitate the development of environmental objectives to support the fish community objectives. Over the years since the signing of the JSP in 1980, efforts to develop quantitative fish community objectives have met with limited success. One of the primary reasons for the lack of success is the failure to adequately link Great Lakes habitat features to the fish populations and communities that depend on these habitats. This has led to the absence of an explicit, ecologically-sound basis for determining the environmental conditions necessary to meet the fish community objectives.

In addition to the needs expressed in JSP, additional needs to link habitat conditions with other ecosystem components have emerged through the Great Lakes Water Quality Agreement (GLWQA; Bertram and Stadler-Salt 2000). In response to the needs implied by this agreement, the State of the Lakes Ecosystem Conference (SOLEC) process was initiated in 1994. Through the SOLEC process, a number of indicators for ecosystem health have been proposed, including measures of Fish Habitat (Indicator #6) and several measures of fish community structure and abundance (e.g., salmon and trout, indicator #8; Bertram and Stadler-Salt 2000). Similar to obstacles experienced in achieving the goals of JSP, there has been little success in linking the fish habitat indicators proposed in the SOLEC process with fish community indicators.

It is easy to argue that achievable fish community objectives must necessarily be based, at least in part, on a consideration of the issue of habitat supply (Rose 2000). To ignore habitat considerations is to implicitly assume that habitat components do not limit the abundance or surplus production available for harvest that can be maintained for the population(s) of interest. Unfortunately, explicit consideration of habitat supply is more easily said than done (Rose 2000). Although numerous studies have been conducted on Great Lakes fish habitat (e.g., HabCARES conference proceedings, Kelso 1996), proven methodologies do not presently exist that link habitat supply to fish population dynamics. The goal of this paper is to present insights we have

gained by developing and evaluating a set of models that explicitly try to link habitat supply measures to fish population dynamics for several Great Lakes fish species.

Habitat "science" is a relatively new discipline within the realm of fisheries management, even though the investigation of abiotic influences on plant and animal populations has long been a central theme of general ecology. Historically, much of fisheries science has focussed on population dynamics, and numerous models exist that reflect our theoretical and applied understanding of demographics and provide a basis for data collection and analysis. Until recently, few models existed that related habitat features to the fish populations depending on those habitats. As a result, the collection of habitat data has been largely descriptive, and habitat management has not been a model-driven process, which has led to subjective decision-making.

To develop fish community objectives based on habitat supply, one needs a model that links habitat components to population status. The simplest models that do this are the well-known habitat-yield models, such as the morphedaphic index (MEI; Ryder et al. 1974), regressions of yield on phosphorus concentrations (Hanson and Leggett 1982) or chlorophyll concentration (Oglesby 1977; Jones and Hoyer 1982). These models describe habitat in a highly aggregated manner (Figure 1). Thus, they are most useful when changes in habitat are of a pervasive nature, such as might occur when phosphorus loadings alter the water chemistry of a large part of a lake basin. These models are also useful when data at a spatially detailed level are absent. Such models are of limited value, however, for examining how changes in localized habitat conditions might affect fish production or yield.

Another approach for linking fish populations to habitat conditions involves the use of Habitat Suitability Index (HSI) models. Data collection for this type of model initially treats habitat conditions at a low level of aggregation (i.e., microhabitat scale; Figure 1). The data are then combined with observations on the distribution of individual fish (often of a particular life stage) to develop utilization curves (e.g., Guay et al. 2000). These curves, in conjunction with expert judgement of species habitat requirements, are used to convert habitat conditions into an aggregated measure of habitat quality, often referred to as weighted usable area (e.g., Williams et al. 1999; Kondolf et al. 2000). The model can then be calibrated against abundance, or more commonly, is assumed to be linearly related to abundance (e.g., Raleigh 1982; Stalnaker et al. 1995). While these types of models permit explicit consideration of a variety of habitat components, they do little to elucidate either the mechanism by which the individual components affect fish populations, or the relative importance of each component (i.e., which component is limiting). Moreover, much of the controversy surrounding these models concerns the rules used to combine the individual suitability curves for different habitat components or for different life stages into an overall index (e.g., Roussel et al. 1999). For example, habitats that provide optimal conditions for one life stage may be sub-optimal for other life stages. Without the link provided by considering the species' population dynamics, it is difficult to justify choices made when combining suitability measures for different life stages. Finally, because these models are calibrated against (or are designed to predict) aggregate indicators of population status such as abundance or biomass, rather than specific demographic parameters such as mortality rates, they

are not well suited to explore the interaction between habitat supply and other factors that affect population dynamics such as biotic interactions or fishery exploitation.

Similar to HSI models, a number of models have been developed that correlate multivariate measures of habitat conditions to fish distribution, habitat utilization, or to indicators of population status such as stock abundance or biomass (e.g., Bowlby and Roff 1986; Wagner and Austin 1999, Stoneman and Jones 2000). These methods provide useful insight into the ecology of fish and their relationship to habitat quality, but they suffer from many of the same limitations as HSI models, especially when used as predictive tools or incorporated into population or community models.

Another suite of models attempts to explicitly link habitat conditions with the vital rates of populations. Although some exceptions exist (e.g., Marschall and Crowder 1996; Minns et al. 1996; Rose et al. 1999), few of these models cover all of the principal vital rates (i.e., birth rate, survival rate, individual growth rate), or follow through the entire life cycle of the model species. Frequently, such models have focussed on a particular life stage or one vital rate (e.g., Brandt and Kirsch, 1993; Mason et al. 1995). The principal goal of the research described here was to use the base these models present to develop models for several Great Lakes fish species that cover all vital rates and the full life history for the majority of these species. We have argued this approach may prove more successful in providing the foundations for a model-based habitat management system (Hayes et al. 1996; Minns et al. 1996). To test the robustness and feasibility of implementing this approach, we selected Great Lakes fish species with contrasting life histories. These species included: walleye (*Stizostedion vitreum*), lake trout (*Salvelinus namaycush*), smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), and steelhead trout (*Onchorynchus mykiss*).

Description of modeling approach

We wish to emphasize that the approach we took in modeling the species selected is not fundamentally different than other approaches that have been previously used (e.g., Marschall and Crowder 1996; Minns et al. 1996; Rose et al. 1999). Rather, using these studies as a base, our choice of specific modeling methods for each species was guided by the situation presented for each species. All models shared a number of common elements, however. A common theme across the models was a focus on population processes of births, deaths and individual growth, leading to a cohort-based, age-structured description of dynamics. In all the models, at least one lifestage was represented as an individual-based model, or a pseudo-individual based model where a cohort was broken into spatially-explicit subgroups. For all of the species, except steelhead trout, we covered the full life cycle of the population of interest. As our modeling efforts progressed, we found that in addition to the key population-level vital rates listed above, the incorporation of fish transport and movement behavior became a vital consideration.

In developing these models, we relied primarily on published studies to relate key processes to

habitat conditions, although a limited amount of field sampling or experiments were conducted for two species. When evaluating relationships presented in the literature, we made an attempt to explicitly characterize effects as density-dependent or density-independent, recognizing that factors that operating in these different fashions have different implications for population dynamics (Hayes et al. 1996).

Overview of individual species models

Walleye

An overview of the walleye model is presented in Figure 2. One of the key features of the walleye model is that the adult population resides in the Western Basin of Lake Erie during the bulk of the year, but a portion of the population spawns in offshore reefs and another part of the population spawns in tributary rivers. At present, the proportion of the population spawning on reefs and in tributaries is unknown. As such, we apportioned the population equally between reefs and tributaries. The walleye model starts with a given population of adult walleye that produce eggs based on their sex ratio and their size distribution. Spawning times depend on water temperature.

For lake spawners, eggs were deposited in offshore reefs following observations of Roseman (2000). The development of eggs was a function of water temperature, and their numbers were reduced by a constant daily mortality rate during development, plus a depth-dependent episodic mortality during high wind events causing disturbance of the spawning habitat (Roseman 2000, Roseman et al. 2001). Following hatching, larval walleye were assumed to be transported by wind-driven surface water currents (Roseman 2000). Larvae transported offshore were assumed to die, and larvae transported onshore were assumed to remain in the nearshore zone after they arrived. The growth and survival of larvae in the nearshore zone was modeled as a function of water temperature and prey abundance.

Selection of spawning habitat in the Sandusky and Maumee Rivers (the principal rivers used for spawning in the Western Basin) by adult walleye was assumed to occur through a process where the best habitat (defined on the basis of substrate size) was selected first, and after saturation, less preferred habitats were selected secondarily. Survival rate of eggs varied with substrate size, and the development rate of eggs varied with water temperature. After hatching, the survival rate and downstream transportation rate of larvae depended on river discharge and temperature, following Mion et al (1998). The growth of larvae while in the rivers was assumed to be negligible because of the lack of zooplankton for first-feeding prey.

After reaching the lake itself, river-spawned larvae were assumed to be exposed to the same environmental conditions as reef-spawned larvae, although their size distribution frequently differed due to differences in spawning times. Larval and juvenile walleye growth and survival during the first year of life were modeled as a function of density and food abundance. We found

no quantitative information in the literature to suggest how other habitat elements (e.g., macrophytes, substrate size composition) affect the growth, survival or distribution of walleye during the first year of life.

Following the first winter of life, changes in growth rate were assumed to be the primary effect of differences in habitat conditions. The principal habitat conditions determining the growth rate of juvenile and adult walleye were light, temperature, and prey abundance, with light and temperature defining the volume of the lake where habitat conditions were acceptable. Mortality rate was assumed to be a constant rate of natural mortality plus fishing mortality on fish of legal size/age.

Smallmouth bass

The study lake was divided into a series of subsections and the habitat characteristics of those subsections are entered into the model. The model then used this information to calculate suitability ratings for nesting and the juveniles/adults to different sites throughout the lake. Ideal free distribution theory (e.g., Fretwell and Lucas 1970) is used to determine the spatial distribution of nests, juveniles and adults throughout the lake (Figure 3). Growth is density-dependent for all life stages. Mortality is size-dependent in the young-of-the-year (YOY) but is set at a constant annual rate for older fish. The model was programmed using Microsoft Visual Basic; thus it can be implemented as a user-friendly tool for fisheries managers.

Lake trout

Egg deposition by adult, wild-spawned lake trout is dependent on the size and age distribution of the adult population (Figure 4). The initiation of spawning behavior is triggered by suitable water temperature, and spawning sites are selected based on substrate size composition and water depth. Egg development is temperature-dependent, and survival of eggs and yolk-sac fry depends on the magnitude of wind-induced water current velocity and the amount of sediment resuspension. After emergence, early juveniles are transported by wind-induced currents, but are able to maintain their location within several weeks of emergence. The growth and survival of juvenile lake trout is modeled as a function of water temperature and food abundance. Modeling of post-juvenile lake trout remains to be completed.

Yellow perch

As with the walleye model, the egg deposition by yellow perch in Long Point Bay depends on the size structure and sex ratio of the population in the eastern basin (Figure 5). Spawning sites are selected based on substrate characteristics, water depth, and the presence of macrophytes (Weber and Les 1982, Fisher et al. 1996, Robillard and Marsden 2001). The timing of spawning is based on water temperature. The development of eggs following deposition is temperature-dependent, and their survival is based on temperature and wind-induced currents and wave action

(as determined by wind speed, wind direction and fetch).

Following hatching, planktonic, larval yellow perch are distributed by water currents, and their growth and survival is determined by water temperature and habitat-based, indirect measures of zooplankton prey abundance (Ross et al. 1977). After reaching approximately 30 mm, juvenile yellow perch become demersal and are no longer vulnerable to relocation by water currents. Survival and growth are dependent on temperature at depth, substrate as a index of food availability, and macrophyte density as a surrogate for relative predation risk. We have also included options for density-dependent growth and survival. As juvenile yellow perch age and grow, they become increasingly able to select preferred habitats, and the model allows for such movements. As adults, yellow perch are modeled as being able to select preferred habitats, and as with juveniles, their growth becomes largely based on temperature and relative food availability in a density-dependent fashion. Options for self-regulation of local population density have also been included in the model. Mortality for juveniles and adults is based on their growth, and also included fishing mortality.

Steelhead

Unlike our other target species, we did not construct a full life-cycle model for steelhead, and because this species was added later in the project, the model is not yet fully completed. Our approach for this species was different than the others because of outside funding that was used to collect field data on habitat conditions and juvenile steelhead response to habitat conditions in the Pine River, Alcona County, Michigan. To date, our focus has been on the dynamics of age-1 steelhead (Figure 6), emphasizing their movement dynamics in response to habitat conditions. A submodel representing potential mechanisms influencing their movement has been created, allowing for predictions of steelhead distribution under various model assumptions. An evaluation of the model assumptions was consistent with field observations. To date, three different movement rules have been evaluated for a subset of our field data. These movement rules include (1) a fixed probability of movement out of each habitat unit (2) probability of movement varying among mesohabitat types (i.e., pool, riffle, run classifications) (3) probability of movement varying as a function of fish density. We are currently developing functional forms to incorporate an interaction between habitat-dependent movement probabilities and density-dependent movement probability. We anticipate that the effects of temperature will also be incorporated following additional data analysis.

As we develop the steelhead model further, we anticipate incorporating the factors shown in Figure 6. In particular, we hope to incorporate temperature-dependent growth, survival and movement, and to incorporate the observed patterns of habitat selection shown by age-1 steelhead.

Insights and perspectives

One characteristic designed into all of the models we developed is that the key population processes (i.e., vital rates such as birth, death, and individual growth rate) are explicitly linked to measurable proximate environmental factors experienced by individual fish. Although these links could have been built into the models in a number of different ways, we chose to portray their dynamics through an individual-based model for the early life stages of our test species. While other, more aggregated representations of these dynamical processes are possible, we found it convenient and effective to use an individual-based approach because it allowed us to readily represent the spatial distribution of individuals within the population. Explicit incorporation of the spatial distribution of individuals was necessary to represent the range of environmental conditions experienced by individuals in the population, and to model changes in their distribution in response to environmental conditions. Although we initially proposed to avoid the extreme reductionism and data demands of individual-based models, we found that this approach was “natural” for the problems we sought to address. As such, we agree with the recommendations of Lomnicki (1999), Juanes et al. (2000), and Rose (2000), among others, that individual-based models are generally the best approach currently available for addressing questions on the linkage between (fish) populations and their habitat. A further advantage of the individual-based approach is that this modeling approach is amenable to the incorporation of factors such as fishery harvest directly into the model. Although we have consciously not included interspecific interactions in order to limit the complexity of our models, we feel that the modeling approach is robust enough to readily incorporate such factors. A final advantage of the individual-based approach is that they tend to favor conceptual simplicity over computational and analytical simplicity or elegance. This conceptual simplicity greatly facilitates the communication and discussion of our model structure to scientists and policy makers.

Another feature common to all of our models is the occurrence of ontogenetic shifts in habitat requirements, emphasizing the need to consider connectivity and spatial patterns of habitat conditions. The fact that different life stages often have different habitat requirements and limitations implies that simple HSI models are likely to be seriously deficient unless some approach to connect the dynamics of different life stages can be implemented with the HSI framework.

Although births and deaths are the only processes directly affecting abundance, we found that the process of fish behavior and their movement or transport among habitats is critical in this modeling approach because this defines which habitats are used and what environmental conditions the individual fish face. For all species, this was one of the greatest challenges we faced in our modeling efforts. Typical of many fish (e.g., Quinlan et al. 1999), the movement of early life stages of these species occurs through passive transport by water currents. Thus, for example, we found ourselves in the position of having to represent surface water currents in the Western Basin of Lake Erie in order to predict transport of larval walleye, and likewise to portray the movement of water across the spawning shoals of Lake Superior for lake trout. Although some models of wind-generated water currents in the Great Lakes exist, none were available for the particular regions inhabited by our target species. Further, even if models were available, the

prediction of fish transport may not be improved. This occurs because water currents in large lakes have a complex 3-dimensional pattern (e.g., Saylor and Miller 1987; Royer et al. 1987). Thus, at a given 2-dimensional location (i.e., latitude and longitude), water current velocity and direction varies with depth and lake bathymetry (Schwab and Bennett 1987; Dave Schwab, Great Lakes Environmental Research Lab, Ann Arbor, MI, personal communication). For example, surface currents may run at 0.1 meter/second in a SW direction, but the current at 5 meters in depth may run 0.05 m/second in a NE direction. The vertical distribution of larval fishes is generally not well known, and further, can vary even on a diel basis (Houde 1969; Hayes, personal observation), possibly in response to water currents (Houde 1969). Thus, the problem of predicting the passive transport of larval and juvenile fishes in the Great Lakes remains a major challenge.

As fish age and are able to actively move against water currents, the situation becomes no less complex. A number of theories, such as optimal foraging theory (e.g., Mittelbach 1981) and the ideal free distribution (e.g., Tyler and Hargrove 1997), have been developed to predict the habitat choice and equilibrium distribution of fish in a heterogeneous environment. Unfortunately, the constantly changing mosaic of environmental conditions results in a transient state of habitat dynamics, a situation where these theories are not readily applicable. One strength of our modeling approach is that the models provide predictions of transient dynamics as well as equilibrium outcomes. For one species (steelhead), a major ongoing component of our field work is to perform tagging studies combined with experimental translocation to better understand the transient dynamics of fish movement and habitat selection (see attachment). In general, we found that habitat selection at the mesohabitat (i.e., pool, riffle, run) level by river-dwelling fish tended to be somewhat easier to handle than for lake-dwelling fish because rivers can be treated as linear geographic features with directional flows, whereas location within a lake is a 3-dimensional geographic feature.

A major challenge we faced in all models was finding published studies relating population vital rates to habitat conditions. For example, a number of studies have documented that recruitment of walleye is correlated to the rate of springtime warming and the severity of wind events (Busch et al. 1975; Roseman 2000). While these studies suggest a linkage between aggregated descriptions of habitat conditions and recruitment success, they provide little information regarding how survival rate of juvenile walleye (for example) varies with water temperature, or how egg survival rate on reefs varies with wind and water velocity. Likewise, there are abundant data describing the habitat conditions where fish are collected, putatively indicating habitat selection, but these data also provide little insight into how population vital rates vary across habitats.

It is difficult to determine the reasons why there are so few studies relating population processes to habitat conditions. We offer two explanations for this observation (1) scientists generally don't conceptualize or frame fisheries problems this way (2) it is difficult to measure mortality and growth rates for fish over short enough time scales to assign these rates to particular habitat conditions. We hope that papers like this will help shape scientists' thinking

when developing studies of fish-habitat relations. The second impediment, however, remains a challenge to fishery scientists and fish ecologists. In the context of this study, we have conducted limited field observations and experiments to provide habitat-specific estimates of vital rates. Our experience with these field studies has provided several insights. First, growth rate estimates are relatively easier to obtain over short intervals than other vital rates. Partly this occurs because the unit of observation is individual fish. Individual tagging provides a means of estimating growth rate of individual fish, thereby providing the possibility of obtaining point estimates and even the distribution of growth rates under specified habitat conditions. Estimating habitat-specific mortality rate, however, has proven much more difficult. Partly this occurs because losses due to mortality are often confounded with movement out of the habitat units. This is particularly a problem in “poor” habitat where fish often move away from such conditions before mortality takes place. Further, mortality rates are often estimated for the (sub)population as a whole, making the unit of observation the (sub)population; as a consequence, many experiments need to be conducted in order to determine variability within the population. Finally, under “good” habitat conditions, mortality rates can be very low, and difficult to estimate precisely for short time intervals.

One linkage between the type of studies identified above and our modeling approach is the possibility of using inverse modeling techniques (e.g., Parker 1977; Nibbelink and Carpenter 1998) to infer vital rates that are consistent with field data. In many cases, prior studies contain data that were collected at a more aggregated level than our level of treatment (e.g., growth and survival of individual fish depends on microhabitat conditions). In inverse modeling, trial values of system parameters are evaluated and adjusted to match observed data, thereby allowing us to sometimes make inferences on processes that are not directly observed. This is a particular advantage if field data were not collected on a habitat-specific level, modeling inferences can be developed to “explain” the observations. While this is a powerful and useful approach, several caveats must be kept in mind. First and foremost, it is often very difficult to resolve among competing model structures. Thus, the inferences being made are conditional on having the “right” model structure in place. Further, parameters are often highly confounded if the level of data resolution (spatial, temporal, or level of process description) does not match that represented

in the model. The level of confounding, if any, depends on details of model structure and the data itself, and as such, each situation needs to be individually considered.

In addition to a dearth of studies relating vital rates to habitat conditions, data for many of the critical environmental/habitat conditions are lacking at a “reasonable” temporal or spatial scale and sampling intensity to be useful. Temporally intensive data collections tend to be spatially very limited, and conversely spatially extensive data tend to be limited to few time periods. Because of this, we often had to use some means for describing habitat conditions based on sparse data. We used two approaches for describing the dynamics of habitats (1) process-driven approach where we model the underlying factors driving habitat conditions (e.g., circulation modeling in lakes) (2) data-driven approach where habitat conditions at an arbitrary time are estimated by interpolation at surrounding times/locations

In the first approach, mechanistic sub-models representing the underlying dynamics of habitat conditions were developed. An example of this is the wind-driven, water current sub-model we used for Lake Erie walleye. In this sub-model, water current velocity and direction were predicted from data available on wind speed and direction. Our representation was by necessity relatively simple; more sophisticated circulation models have been developed, but are not readily transferrable to our particular problem. One strength of this approach is that data on the habitat conditions of interest are not required if data on other, driving variables are available.

In the second approach, habitat conditions over the entire region are interpolated from existing data. This too creates a model of habitat dynamics, making assumptions regarding how these conditions vary across space and time, but these assumptions are not based on driving mechanistic processes because data are directly available for the variable of interest. For example, point water temperature data for Long Point Bay were available at a limited number of locations and times. With these data and satellite imagery of the entire bay, an interpolation model predicting the water temperature at intermediate times and locations was constructed. This model assumed substantial coherence in temperature patterns at a large spatial scale, but finer scale patterns (e.g., upwelling events) were generally preserved by the combined information from temperature dataloggers and spatially-explicit thermal imagery. Interpolations further assume some regularity in the vertical temperature structure during the summer stratification period. We feel that such assumptions are reasonable in many situations, where there are data available and models for predicting thermal structure are not readily available. Even a coarse estimate of temporal and spatial differences in physical variables (especially temperature) is more realistic than using a single profile to represent an entire water body. In general, we feel that the interpolation approach is particularly useful when data on habitat conditions are available at a reasonable sampling intensity to predict interpolated points, and when the habitat conditions themselves are relatively continuous and coherent across space and time. An example of where the interpolation approach is less useful is predicting water currents, which often show abrupt changes at time scales much shorter (e.g., hours to days) and spatial scales (e.g., within 1-2 meters vertically) than sampling generally takes place.

The broad time scale across which habitats vary also presents several challenges. For example, temperature patterns in the environment often change over short time periods (e.g., days), but other features such as bathymetry or channel morphology often change slowly (e.g., years to decades). This can result in “stiff” systems (borrowing the term used for differential equations; Press et al. 1992) where the dynamics of different components need to be treated differently. The varying time scales for habitat variation also has implications for sampling intensity necessary to represent habitat conditions adequately. Some features, such as bathymetry, are likely to change relatively slowly, allowing for sampling to be temporally less intensive. Other features, such as stream water temperature, which may vary several degrees within a day, may require almost constant measurement. Most challenging, perhaps, are habitat conditions that rapidly vary both spatially and temporally. Water temperature in Great Lakes embayments is an example of such a situation. During periods of stratification development or decay, the water temperature at a given point can change within a few days, and the difference in temperature between adjacent points (e.g., points along a vertical thermal profile) may likewise change rapidly. Cases such as these are difficult to address with either mechanistic models or interpolation models because of the abrupt changes that may occur. Therefore, the choice of time step in habitat-based models is important, as well as the availability of data or physical models as input.

Across our model species, several habitat features showed a pervasive effect on model outcomes. Foremost among this is water temperature (Magnuson et al. 1979). Water temperature has long been known to strongly affect growth (e.g., Kitchell et al. 1977; Hewett and Johnson 1992), survival and development rate of fishes (e.g., Allbaugh and Manz 1964, Hurley 1972), and further can strongly affect their spatial distribution (e.g., Mason et al. 1995). Because of its effect on multiple vital rates and fish behavior, changes in water temperature can have a disproportionate effect on aggregated outputs such as production, biomass and abundance. As such, obtaining adequate data on spatial and temporal variability in water temperature should be a priority for habitat investigations.

Another habitat feature that had an important role in each of our models was water currents. Although adult fish are generally able to avoid strong currents, or maintain their position against such currents, the survival of eggs and the distribution and survival of larvae and early juveniles is often strongly affected by water currents (e.g., Houde 1969, Clady 1976). Unfortunately, data directly measuring water current velocity in the Great Lakes or their tributaries are often lacking, and tend to be expensive to collect. Moreover, water velocity and direction in the Great Lakes is very dynamic, often changing over the course of hours to days, and over short spatial scales (e.g., 1-2 meters within a vertical profile). Circulation models are a helpful tool to address this problem,

but are a major task in and of themselves.

We have focused on process-driven, mechanistic models, in contrast to aggregated, holistic models (such as MEI). We do not mean to imply that the mechanistic modeling excludes aggregated modeling - rather, the two approaches should be able to inform one another. For example, the process-driven models can help identify mechanisms that give rise to the observed aggregate patterns. Likewise, the observed aggregate relationships are important validation data for the mechanistic models. A strength of our modeling approach is that the model explicitly makes predictions for many system attributes, ranging from process rates (e.g., birth rate, death rate, individual growth rates) to detailed descriptions of system characteristics (e.g., distribution of fish), to more aggregated descriptions of the system (e.g., total biomass, abundance, population size structure). Comparison of model predictions across this range of scales with data helps to validate the models and point to the specific areas where there are problems. This is in contrast to regression-based approaches where it is often difficult to pinpoint how and why the regression may not fit. Despite the conceptual appeal of performing model validations at several levels of aggregation, trying to validate our models has been a very challenging task because of the limited data available for validation. Further, a key use of these models is to predict the response of fish to changes in habitat conditions; conditions that may be outside the range of data used to construct the models. As such, validating models for this purpose may be virtually impossible. This does not imply that such models are useless; rather, the use of these models (or any other model used to make similar predictions) should recognize the uncertainty associated with such situations.

While constructing our models, we often made trade-offs between basing the model on data versus assumptions. Because of the lack of published studies, we were often “forced” into making assumptions to get the most basic model to run. A hard question to answer is “when are there so many assumptions, or when are the assumptions so strong, that the model predictions are not informative?”. An associated question is how to make good assumptions. One approach for making assumptions that we found particularly appealing was to use general principles from ecology or other basic sciences as the basis making an assumption. For example, in long time periods, fish evolution is a shaping force. This can be a problem because fish can adapt (thereby altering the parameters describing how their vital rates vary with habitat conditions) to changing habitat conditions. In the short term, however, we can use the assumption that fish have adapted to present habitat conditions, and tend to behave in an optimal way (i.e., maximize fitness) to help constrain some of our modeling problems. For example, we used the idea that smallmouth bass spawning distribution will follow the Ideal Free Distribution (e.g., Fretwell and Lucas 1970; Tyler and Hargrove 1997). We assume that they are behaving to maximize fitness, and that some principles of optimal habitat selection guide fish distribution if they are able to actively choose among potential habitats. Another example of using basic ecology to constrain our models is the application of life history theory (e.g., Jensen 1998) to help “tie together” different life stages in our models (Shuter et al. 1998; Lester *et al. in review*). Constraints imposed by life history consideration helped us to infer ages and sizes at maturation of walleye (for example) under different growth regimes imposed by different habitat conditions. These theories help by creating

constraints in the modeling problem, making it much more feasible to find reasonable solutions.

In summary, we feel that the modeling approach we have used holds much promise for bringing forward a useful marriage between the tradition of fish population dynamics and habitat science. Many practical concerns remain, however, not the least of which is the lack of solid quantification of the response of population vital rates and fish behavior to habitat conditions, and the scarcity of data on habitat conditions at a broad temporal and spatial scale. Another challenge not listed above is how to bring this modeling approach into a true multi-species application, where fish populations interact fully with their prey, other populations of fish, and the habitat in which they all reside.

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List of Figures

Figure 1. Modeling approaches for linking fish populations to habitat conditions, emphasizing alternative ways of cutting across different levels of aggregation.

Figure 2. Flowchart of walleye population model, emphasizing key components and driving variables for each life stage.

Figure 3. Flowchart of smallmouth bass population model, emphasizing key components and driving variables for each life stage.

Figure 4. Flowchart of yellow perch population model, emphasizing key components and driving variables for each life stage.

Figure 5. Flowchart of lake trout population model, emphasizing key components and driving variables for each life stage.

Figure 6. Flowchart of steelhead model, emphasizing key components and driving variables for each life stage.

